United States
Department of
Agriculture

Forest Service

Pacific Northwest
Research Station

General Technical
Report
PNW-GTR-213

Models That Predict Standing Crop of Stream Fish From Habitat Variables: 1950-85

Kurt D. Fausch, Clifford L. Hawkes, and Mit G. Parsons

Authors

KURT D. FAUSCH is associate professor of fishery biology, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523; CLIFFORD L. HAWKES is a fishery biologist, Denver Service Center, Western Team, National Park Service, Box 25287, Denver, CO 80225; and MIT G. PARSONS was a fishery biologist, Wildlife and Fishery Ecology Unit, USDA Forest Service, 3825 East Mulberry Street, Fort Collins, CO 80524. Currently Mit Parsons is with the Legislative Affairs Staff, USDA Forest Service, P.O. Box 96090, Washington, DC 20013-6090.

Abstract

Fausch, Kurt D.; Hawkes, Clifford L.; Parsons, Mit G. 1988. Models that predict standing crop of stream fish from habitat variables: 1950-85. Gen. Tech. Rep. PNW-GTR-213. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 52 p.

We reviewed mathematical models that predict standing crop of stream fish (number or biomass per unit area or length of stream) from measurable habitat variables and classified them by the types of independent habitat variables found significant, by mathematical structure, and by model quality. Habitat variables were of three types and were measured on different scales in relation to stream channels: variables of drainage basins were measured on the coarsest scale from topographic maps; channel-morphometry and flow variables were measured in the field along transects perpendicular to flow; and habitat-structure, biological, physical, and chemical variables were measured on the finest scale in the field. We grouped the 99 reviewed models by the types of independent variables found significant during model development: (A) primarily drainage basin (5 models), (8) primarily channel morphometry and flow (16 models), (C) primarily habitat structure, biological, physical, and chemical (25 models), (D) a combination of several types of variables (39 models), and (E) tests of weighted usable area as a habitat model (14 models). Most models were linear or multiple linear regressions, or correlations, but a few were curvilinear functions (exponential or power). Some used multivariate techniques (principal components or factor analysis), and some combined independent variables into one or more indices. We judged model quality based on simple criteria of precision and generality: coefficient of determination, sample size, and degrees of freedom. Most models were based on data sets of fewer than 20 observations and, thus, also had fewer than 20 degrees of freedom. Most models with coefficients of determination of greater than 0.75 had fewer than 20 degrees of freedom, which led us to conclude that relatively precise models often lacked generality. We found that sound statistical procedures were often overlooked or were minimized during development of many models. Frequent problems were too small a sample size, possible bias caused by error in measuring habitat variables, using poor methods for choosing the best model, not testing models, using models based on observational data to predict standing crop, and making unrealistic assumptions about capture probabilities when estimating standing crop. The major biological assumption--that the fish population was limited by habitat rather than fishing mortality, interspecific competition, or predation--usually was not addressed. We found five main ways stream-fish-habitat models are used in fishery management. To be useful for analyzing land management alternatives, models must include variables affected by management and be specific for a homogeneous area of land.

Keywords: Stream fish, fish habitat, predictive models, stream-fish standing crop.

Contents

Introduction

A diverse array of models that predict standing crop of stream fish (number or biomass per unit length or area of stream) from measurable characteristics of the environment have been developed since 1970, although fishery biologists have searched for variables closely linked to fish abundance for at least 35 years (Allen 1951, McKernan and others 1950). Our primary purpose was to review these models and organize their diversity by the types of habitat (independent) variables found significant, the mathematical structure, the size of the data sets used to develop the models, and how well the models fit these data. We included all models developed for fish in natural streams that we could find, as of August 1985., in the primary literature, in reports of State and Federal natural resource agencies, in theses, and from personal sources. We specifically searched the *Sport Fishery Abstracts* (1955-85, volumes 1-30(2); now *Fisheries Review,* Office of Information Transfer, U.S. Fish and Wildlife Service, 1025 Pennock Place, Fort Collins, CO 80524}, but most models were found through personal communication with fishery biologists. We undoubtedly missed some models but have a large, representative sample including the most important and widely used models. Because relatively few models are published in primary fishery or aquatic biology journals, review and comparison by model users and developers has been difficult. We hope this report will aid in that process.

Wesche (1983) describes habitat evaluation as a young, dynamic science characterized by many methods applied in different ways and by a lack of standards for measuring habitat attributes. Because most models are too new to have been adequately tested, we chose not to critically review them but rather to provide basic data for all the models while describing a subset in more detail. We chose the subset based on historical significance, wide use by biologists, or adequate development and testing.

To promote improved models for the future, we have highlighted investigations using sound approaches to model development, testing, and interpretation so that others might follow that lead. A second purpose therefore was to address several important aspects of model building, including proper statistical methods, errors in habitat measurements, and major biological assumptions of models. Finally, we discuss the present uses of models and how researchers might develop more useful models for fishery managers.

Types of Habitat Variables

Physical, chemical, and biological measurements used by investigators as independent or input variables in models can be divided into three categories by the method and scale of measurement. Variables of the drainage basins were measured from topographic maps and were therefore generally of coarse scale in relation to the size of stream channels. These variables included characteristics such as drainage basin area, mean basin elevation, total stream length, drainage density, stream order, and stream gradient (when derived from a map). Most are geomorphic variables used by fluvial hydrologists to predict streamflow and sediment yield and can be found in standard references such as Chow (1964).

A second class included independent variables describing **channel morphometry and flow.** These variables were usually measured in the field along transects perpendicular to streamflow. Examples are various measures of stream discharge (also available from U.S. Geological Survey [USGS] gauge records), width, depth, mean velocity, wetted area, pool volume, and gradient (when measured in the field over a stream reach), and percentages of habitat types (for example, pool, riffle, run). These characteristics are measured on a finer scale than are drainage basin variables.

A third class of variables, **habitat-structure, biological, physical, and chemical** variables, generally related to fish microhabitat. Most of these variables were measured in the field for individual study reaches on the finest scale of the three variable types. This class included the various forms of cover for fish, streambank stability, depth-and-velocity preferences, invertebrate drift abundance, substrate composition, temperature, and measures of water chemistry. Some cover and substrate variables are difficult to measure and often are evaluated subjectively.

Mathematical Structure of Models

Most of the models we reviewed were simple or multiple linear regressions fit by least squares procedures and are of the form:

$$SC = a + bX_1 + cX_2 + \dots + nX_n \; ; \qquad (1)$$

where SC = standing crop of stream fish in numbers or biomass per unit length or area of stream,

$X_1, X_2, \dots X_n$ = independent habitat variables, and a,
a, b, ...n = regression coefficients.

An advantage of these models is that standard statistical procedures can be used to calculate regression coefficients, the confidence and prediction intervals around the regression line, and the percentage of variation in standing crop accounted for by the independent variables in the model (the coefficient of determination, R^2 or r^2). Some investigators simply calculated the correlation between standing crop and a single independent variable.

Other models were more complex exponential functions:

$$SC = a \,.\, e^{bX} \qquad (2)$$

$$(\log_e SC = \log_e a + bX) \; ;$$

or power functions:

$$SC = a \,.\, X^b \qquad (3)$$

$$(\log_e SC = \log_e a + b \log_e X) \; .$$

These equations were transformed to straight lines by using logarithms, as shown in parentheses below each equation, and the coefficients were determined by using simple linear regression. Some of the models reviewed were more complex forms of these equations.

Some modelers combined independent variables into one or more indices and then used regression to calculate a linear, power, or exponential function between standing crop and the index. Finally, some investigators used the multivariate statistical techniques of factor analysis or principal-components analysis to select linear combinations of independent variables that accounted for the most variation in standing crop, thereby reducing the dimensions of the data. These techniques are used to attempt to reveal the important habitat variables, but Johnson (1981) gives several cautions about the use of multivariate statistics for this purpose.

Categories of Models

We first classified the models into five categories according to the types of independent variables significantly related to standing crop of stream fish. The first three categories include the models using primarily one of the three variable types to predict standing crop: drainage basin variables; channel morphometry and flow variables; or habitat-structure, biological, physical, and chemical variables. A fourth category includes models using variables of several types, and a fifth set includes tests of weighted usable area (WUA; see Bovee 1982) as a predictor of standing crop of stream fish.

Tables for each category (tables 1-5, see appendix) give pertinent data about the "best" model each investigator developed for each fish species (or group) and life stage (for example, juvenile trout, adult small mouth bass; see table 6 in the appendix for scientific names), so only one model was chosen when several predicting the same quantity were presented in a paper. Selecting the best models was difficult because most investigators reported only the coefficient of determination (r^2 or R^2 for multiple linear regression) for their models, and few tested whether regression coefficients were significantly different from zero. Very few modelers calculated standard errors for regression coefficients, calculated confidence or prediction intervals around the regression line, or tested their models with other data. Without this information, users cannot determine whether the model is widely applicable or sufficiently precise for their needs. For lack of a better criterion, we therefore selected the model with the highest coefficient of determination as best, even though we will discuss below why we do not recommend this practice.

Model Quality

Because limited information was available to evaluate relative quality among the best models, we initially classified models by two simple criteria: sample size and coefficient of determination. We suspect that even models based on only one or two habitat variables and pertaining to only a limited area or period of time require a data set of at least 20 measurements to represent natural variation in standing crop. Models listed in tables 1-5 are therefore classed by sample sizes of $\geq$20 or $<$20 and are arranged in descending order by coefficient of determination.

Discussion of Models

For each of the five categories of models, we describe a subset that is historically significant, widely used by biologists, or at least adequately developed and tested. Within these groups, the models are numbered, and generally presented, in chronological order (see tables 7 and 8 in the appendix for lists of models by number and author). Model numbers, shown in the text in bold type, correspond to those in tables 1-5, with the first digit indicating the table number. The habitat variables found to be significantly related to standing crop in each model are listed in the tables by abbreviated acronyms, which are defined in table 9 (appendix).

Models Based Primarily on Drainage Basin Variables

Model1.01--Ziemer (1973; **1.01**, table 1) developed a model to predict the escapement of pink salmon spawning in Alaska streams from geomorphic variables of drainage basins. His main tenet was that, within a region of homogeneous geology and climate, certain drainage basin characteristics are related to flow regime and channel morphology which, in turn, control fish production. He measured nine geomorphic variables for 21 streams from topographic maps and assumed that historical counts of pink salmon escapement were adequate measures of potential fish production. Although we did not review in detail other models predicting escapement, we included this one because it is the earliest using only drainage basin variables.

Ziemer (1973) developed two indices of potential fish production from four geomorphic variables affecting runoff. One of the indices was correlated with pink salmon escapement, but no statistical analyses were reported. Although the data are variable, we found that a linear transformation of the power function (see equation 3) derived from Ziemer's (1973) plot of pink salmon escapement as a function of the index accounted for 34 percent of the variation, when three outliers he identified were excluded.

Models 1.02 and 1.03--Using a similar approach, Burton and Wesche (1974; **1.02**) and Wesche and others (1977; **1.03**) developed indices from drainage basin variables and related them to standing crops of brook trout, brown trout, rainbow trout, and Colorado River cutthroat trout in Wyoming streams. They show that at least part of the variation among standing crops of salmonids can be accounted for by drainage basin variables such as mean basin elevation and total stream length.

Models 1.04 and. 1.05--Lanka (1985; see also Lanka and others 1987) developed models to predict standing crops of four species of trout in high-elevation forested streams (**1.04**) and low-elevation grassland streams (**1.05**) in Wyoming. His objecttives were to evaluate relations among drainage basin geomorphology, instream habitat, and trout standing crop and to make models allowing fishery managers to rapidly estimate standing crops from easily measured variables. For each stream type, he built three models using 11 drainage basin variables, 10 instream variables (a combination of variables including channel morphometry, velocity, substrate, and channel stability), or all 21 variables. Historical data were gathered from several sources, and Lanka (1985) collected additional data to test the models.

For both stream types, Lanka (1985) chose the best models based on the highest adjusted R2, an objective criterion described below. In both cases, the best model included one instream habitat variable and three drainage basin variables. Relative prediction error (the. predicted standing crop minus the actual standing crop, divided by the predicted standing crop) was lower for all models when the data collected for model tests were used than when original data for model development were used.

Lanka (1985) also discussed biological mechanisms whereby variables included in the models could affect the standing crop. Canonical correlation analysis indicated a significant relationship between drainage basin variables and instream variables, which suggested to him that the relation between drainage basin geomorphology and the standing crop of trout results from a functional link between geomorphology and instream habitat.

We propose that this category of models is most useful for basinwide planning and analysis in fishery management. Although most of the models appear relatively imprecise, when judged solely from the coefficients of determination (table 1), Lanka (1985) found relative prediction errors of 39 percent for the best model for rangeland streams, and only 18 percent when the model was tested. He suggested that the separation of basins into two homogeneous groups improved model performance. Other modelers used drainage basin variables to separate good and poor spawning streams for Pacific salmon in Alaska by using discriminant functions (Swanston and others 1977) and to predict habitat quality for anadromous salmonids in Oregon under natural and managed conditions (Heller and others 1983, Parsons and others 1981).

Models Based Primarily on Channel Morphometry and Flow Variables

Models 2.01 and 2.02--Since 1950, several investigators have related catches and escapement of anadromous Pacific salmon (Brett 1951, McKernan and others 1950, Scarnecchia 1981, Vernon 1958, Wickett 1958), striped bass (Stevens 1977), and chinook salmon, American shad, and longfin smelt (Stevens and Miller 1983) to river flows and other climatological conditions, such as rainfall and ocean upwelling (table 2). Similarly, Bulkley and Benson (1962) and Drummond (1965) found that indices of year-class strength for cutthroat trout were significantly related to indices of stream-flow during spawning, incubation, or rearing. Burns (1971), however, was the earliest reference we found who related standing crop of stream fish to variables of channel orphometry and flow. He found that surface area accounted for 81 percent of the variation in standing crops of anadromous salmonids (**2.01**) and 80 percent of the variation for all teleosts (**2.02**) in northern California streams.

Model 2.03--Hunt (1971; **2.03**) correlated standing crops of brook trout in 17 sections of a Wisconsin stream to five channel morphometry variables and overhead bank cover for 3-year periods before and after the habitat was improved. In eight multiple correlations, these six variables accounted for 59-85 percent of the variation in numbers or biomass of trout. Pool area and bank cover were the most important variables, the two together explaining 68 percent of the variation in number of trout larger than 6 inches after habitat enhancement.

Models 2.06 and 2.07--White and others (1976; **2.06, 2.07**) related populations of brook trout and brown trout in six Wisconsin and Michigan streams to seven streamflow variables and two measures of standing crops from previous years. Latta (1965) had shown that groundwater level, assumed to be related to baseflow discharge, accounted for 71-74 percent of the variation in fall numbers of age-0 brook trout for 9 years in a Michigan stream, but accounted for relatively little of the variation in abundance of age-0 brown trout. In contrast, White and others (1976) found no significant relationships between abundance of age-0 brook trout and flow variables when they used 17 years of data then available for the same Michigan stream, although a multiple regression of numbers of age-0 brown trout on flow variables explained 37 percent of the variation.

Significant regressions of numbers of fall age-0 trout on flow and previous standing crop variables for four of the six streams White and others (1976) studied accounted for 66-95 percent of the variation in standing crop (**2.06**). Similarly, all but one multiple regression of total trout biomass on similar variables accounted for 50-94 percent of the variability (**2.07**). They concluded that high, stable stream discharge and lack of severe floods, especially in winter, are favorable conditions for trout in midwestern streams.

Models 2.05, 2.08, 2.09, 2.10, and 2.14--Several investigators have found significant relationships between stream salmonid populations and flows. In Wisconsin, White (1975 ; **2.05**) found more brook trout and brown trout in years when flow was high the previous winter, and Hunt (1979; **2.08**) found more brook trout during the fall after summer base flow was high. Similarly, Nelson (1980; **2.09**) showed that trout populations in the Gallatin River, Montana, were related to minimum summer flows; and Solomon and Paterson (1980; **2.10**) found more age-0 brown trout when April flows were high in two English chalk streams. Frenette and others (1984; **2.14**) report that Atlantic salmon parr numbers were related to periods of critical spring and summer low flow in a Quebec river. These studies indicate that inadequate base flows can be a limiting factor to stream salmonid populations by reducing suitable microhabitat.

Models 2.11, 2.12, and 2.13--In contrast to the researchers who found that low flows limit salmonid populations, Nehring and Anderson (1981,1982,1983,1984; **2.11, 2.12, 2.13**) report that high flows in several Colorado rivers during incubation or soon after emergence reduced year classes of brown trout (**2.11, 2.12**) and rainbow trout (**2.13**) by washing away eggs or fry. For each river where long-term population estimates were available, they found strong negative correlations between year-class strength and high flows during these critical periods. In other river reaches, especially those below reservoirs, they found that flow fluctuations leave salmonid redds without water during the winter, which also reduces year-class strength.

Models 2.04 and 2.15--Kraft (1972; **2.04**) experimentally reduced flows in several sections of a Montana stream and found that the number of brook trout remaining was related to channel morphometry and cover variables. Randolph and White (1984; **2.15**) also manipulated flows in a Montana stream to test the validity of using the wetted perimeter method to make instream flow recommendations. They measured decreases in habitat and fish abundance associated with reductions in flow and found that the number of rainbow trout remaining in two of three sections lagged decreases in discharge; the highest correlations were between fish remaining and flow 11 and 15 days previous.

Model 2.16--Chisholm and Hubert (1986; 2.16) found that standing crops of brook trout in 13 southern Wyoming mountain streams were largest in reaches having the least gradient. Four channel-morphometry variables accounted for 69 percent of the variation in brook trout biomass over a gradient range of 0.4-9.2 percent.

Because channel-morphometry and flow variables often require field measurement, models based primarily on these variables require an intermediate amount of effort to apply. This extra effort should increase the precision of prediction substantially, if we judge solely by the coefficients of determination of the 16 models using this variable type exclusively (table 2), at least when models are developed for relatively small geographic areas. Where USGS gauge records are available for reaches of interest, models based on flowean be more easily applied. Nehring and Anderson (1984) suggest, as an example of model use, that populations of age-0 brown trout could be augmented by stocking when year-class failure is predicted from high spring runoff flows in a Colorado river.

Models Based Primarily on Habitat-Structure, Biological, Physical, and Chemical Variables

Model 3.01--McFadden and Cooper (1962; **3.01**, table 3) related salmonid and nonsalmonid standing crop to conductivity in six Pennsylvania streams and found that the partial correlation between nonsalmonid biomass and conductivity, given the total number of fish species, accounted for the most variation. Although their best correlations were significant only at $P \leq 0.25$, they do suggest a relationship between fish standing crop and conductivity or other correlated variables like alkalinity that indicate stream productivity. This study is the earliest attempt we could find that relates stream-fish standing crop (rather than catch or escapement) to measurable environmental variables.

Model 3.03--Enk (1977; **3.03**) developed linear regressions to predict standing crops of brook trout and brown trout in two Michigan streams from the length of overhead bank cover that met Wesche's (1974) criteria. The criteria are for the bank to be at least 9 cm wide and to have at least 15 cm of water beneath it. A maximum of 88 and 93 percent of the variation in trout biomass was explained by the one cover variable for the two streams.

Models 3.02, 3.05, and 3.15--Like Enk (1977), several other investigators also developed models predicting standing crops of stream salmonids from relatively simple measures of cover. Klamt (1976; **3.02**) found a significant multiple correlation between density of salmonids (primarily age-0 chinook salmon) and two independent variables, boulder-and-log cover and abundance of drifting invertebrates, in two Idaho streams. Several models that included percentage of fine sediment in riffles also contained a ratio of variables (drift per pool area) but Klamt (1976) reported that this may cause statistical complications. Ward and Slaney (1980; **3.05**) report a signify-cant correlation between abundance of rearing steelhead parr and the number of boulders in a .river on Vancouver Island, British Columbia. Gordon and MacCrimmon (t982; **3.15**) found that density and biomass of juveniles of anadromous brown trout, coho salmon, and steelhead correlated significantly with instream and permanent bank cover in a tributary to Lake Eire in Ontario.

Model 3.04--Harshbarger, and Bhattacharyya(1981 ; **3.04**) measured 18 characteris-tics of cover for trout (species not reported, but most likely brook trout and rainbow trout) in 100 sections of five streams in North Carolina. They used factor analysis to determine six factors (linear combinations of the 18 original variables) that best described the data. Both the factors and the original variables were then used in multiple regressions to predict standing crop. They found that the six most significant independent variables explained more variation in standing crops of four age classes of trout (maximum of 66 percent) than did the six derived factors. Variables common to all the models were the number of rocks affording cover, percentage of brush cover, and. percentage of cover as bank vegetation trailing in the water.

Models 3.06 and 3.07--Wesche (1980; **3.06, 3.07**) developed a model that predicts standing crops of brown trout for Wyoming streams as a function of a trout-cover rating. The rating is calculated from length of overhead bank cover; area of rubble, boulder, or aquatic vegetation substrate; the preference of trout species for these two habitat features; and in larger streams (>100 ft^3/s mean discharge), the area of water deeper than 1.5 feet. These variables were combined in two indices accounting for 60 percent of the variation in biomass in reaches of eight small streams (**3.06**) and 95 percent of the variation in biomass in four large streams **(3.07**). No significant relationships were found for brook trout at 9 sites or for Colorado River cutthroat trout at 12 sites, so Wesche (1980) concluded that populations of these species are not controlled as much by cover as are other species.

In an earlier test of the cover rating, Wesche (1974, 1976) found that standing crop of the same three trout species (brook, brown, and Colorado River cutthroat) was an exponential function of the trout-cover rating for small streams, but the coefficient of determination was not reported even though the regression coefficient was signify-cant. These studies indicate that many forms of cover can significantly affect popula-tions of stream salmonids when other factors are not limiting.

Models 3.08-3.12--Barber and others (1981 a; **3.08-3.12**), Barber and others (1981b), and Oswood and Barber (1982) predicted standing crops of four fish species in southeastern Alaska streams from physical microhabitat variables measured by using a standard transect method and a technique they developed to map areas of different microhabitats within sections. They found their area method to be superior and developed a multiple regression model (3.08) accounting for 76 percent of the variation in standing crops of age-0 coho salmon from three independent variables: $\log_{10}$ available spawning area, area of overhanging vegetation, and the number of days from June 1. When they calculated principal components using all 17 measured variables, and used these principal components as independent variables in multiple regressions, 81 percent of the variation in number of age-0 coho salmon was accounted for. They also developed ,similar models for age-1 coho salmon (3.09), Dolly Varden (**3.10**), coastal cutthroat trout (**3.11**) ,and coastrange sculpin (3.12), but only the models not using principal components are listed in table 3. For Dolly Varden and coastal cutthroat trout, multiple regressions based on the transect method had higher coefficients of determination than those based on the area method.

Model 3.13--Several investigators developed models that predict stream-fish standing crop primarily from measures of stream substrate. Paragamian (1981; **3.13**) predicted abundance and biomass of juvenile and adult smallmouth bass in an Iowa river from the percentage of area with exposed substrate of 16-256 mm. An exponential function best fitted the relationships, and accounted for 41-90 percent of the variation in biomass and numbers of smallmouth bass in two different years. Paragamian (1981) is one of the few investigators reporting standard errors and confidence intervals for regression coefficients.

Model 3.14--Eifert and Wesche (1982; **3.14**) evaluated several habitat quality indices (Binns 1979, Duff and Cooper 1978, Pfankuch1975) as predictors of brook trout, brown trout, and rainbow trout in two Wyoming streams; they found that these indices generally accounted for 50 percent or less of the variation in standing crop. Their best model, though, is based on the area of substrate composed of rubble, boulder, or aquatic vegetation--a variable from Wesche's (1980) trout-cover rating that accounted for 71 percent of the variation in fish standing crop.

Models 3.16 and 3.17--Hawkins and others (1983; **3.16, 3.17**; see also Murphy and others 1981) related density and biomass of stream salmonids (coho salmon, cutthroat trout, and steelhead trout) and sculpins (coastrange sculpin, prickly sculpin, and reticulate sculpin) to percentage of fine sediment in riffles and density of collector-gatherer invertebrates in riffles. At shaded sites, they found a highly significant negative correlation ($P<0.01$) between salmonid density and riffle sediment (**3.16**), and a highly significant positive correlation ($P<0.01$) between sculpin biomass and density of collector-gatherer invertebrates (**3.17**).

Models 3.18-3.22--Stowell and others (1983; **3.18-3.22**) compiled equations, based on data from other sources, predicting fry emergence and summer and winter rearing capacity for juvenile steel head trout and chinook salmon in Idaho rivers from percentage of embeddedness of the stream substrate. The embeddedness resulting from fine sediments eroded from these watersheds is predicted from the increase above natural sediment yields due to timber harvest and associated activities with the sediment-yield model of Cline and others (1981). In general, the models predict density of summer- and winter-rearing steel head juveniles (**3.18, 3.19, 3.22**) and chinook juveniles (**3.20, 3.21**) as negative exponential or polynomial functions of embeddedness, and account for 87-99 percent of the variation in standing crop of the two salmonids. All the models based on measures of substrate show that many stream fish are dependent on specific substrates for spawning and for hiding cover for juveniles and adults.

Models 3.23, 3.24, and 3.25--McClendon and Rabeni (1985; **3.23,3.24, 3.25**) related density and biomass of three centrarchids in a Missouri Ozark river to 31 variables of all three types. They constructed models for adult smallmouth bass (**3.23**), rock bass (**3.24**), and longear sunfish (**3.25**) from data for 10 sites. They measured habitat and fish populations at 10 more sites to test the models and then combined all the data to calculate a new model. Most models performed well in this validation, and the best two- or three-variable models accounted for about 60 percent of the variation in standing crop. McClendon and Rabeni (1985) found that habitat structure and substrate variables were significant in models most often.

Models based primarily on habitat-structure, biological, physical, and chemical variables require the most effort to apply because field measurement of these variables is generally time consuming. When judged solely by coefficients of determination, some models performed very well but others were less precise. Those performing well generally apply to only a few streams or rivers or to a specific life history stage where fish are limited by one or a few environmental variables.

Models Based on a Combination of Variable Types

Many models predict standing crop of stream fish from a combination of variable types (table 4). Nine models from this group are based primarily on measures of channel morphometry, cover, or substrate.

Model 4.01--Lewis (1969; **4.01**) developed a model to predict standing crops of brown trout and rainbow trout in pools of a Montana stream as a function of pool area, width, depth, current velocity, cover area, and percentage of cover. Mean, current velocity and cover area accounted for 66 percent of the variation in numbers of both total trout and brown trout in pools, and current velocity alone explained 51 percent of the variation in the number of rainbow trout. From the significance of individual variables in regressions, Lewis (1969) inferred cover to be most important to brown trout and current velocity to be most important to rainbow trout, a conclusion coinciding with knowledge about the ecology of these species.

Models 4.02, 4.03, 4.08, 4.26, and 4.39--Stewart (1970) developed models to predict standing crops of brook trout (**4.02**) and rainbow trout (**4.03**) in a Colorado stream from mean depth and cover variables. Rinne (1978; **4.08**; see also Rinne 1981) related standing crop of Gila trout in a New Mexico stream to several channel morphometry and cover variables. Konopacky (1984; **4.26**) made models to predict biomass of age-0 chinook salmon in pools of several Idaho streams from measures of channel morphometry and stream substrate. Marshall (1985; **4.39**) constructed two models to predict fall biomass of fingerling brown trout stocked in Iowa streams from four easily measured variables of channel morphometry, cover, and substrate.

Models 4.10, 4.11, and 4.12--Nickelson and others (1979) developed models to predict standing crops of cutthroat trout (**4.10**), juvenile steelhead trout (**4.11**), and juvenile coho salmon (**4.12**) in Oregon streams primarily from variables of channel morphometry, flow, and habitat structure. As an example of the models (**4.10**), they created a total-cover variable for cutthroat trout by summing the frequencies of suitable depths, instream cover, overhanging cover, surface turbulence, and velocity refuge, measured at points along transects. They multiplied this variable by a factor reflecting the suitability of section velocity for cutthroat trout and by section area, yielding a habitat quality rating (HQR), which they used as the independent variable to predict standing crop. Two slightly different HQR's accounted for 87 and 91 percent of the variation in standing crop of cutthroat trout; 48 and 57 percent of 20 new observations collected to test the models fell within the 95-percent prediction interval for the original regressions. A similar model was developed for juvenile steelhead trout (**4.11**).

Pool volume alone accounted for 93.5 percent of the variation in juvenile coho biomass (4.12), and 88 percent of 318 new sections measured to test the model fell within the 95-percent prediction interval. A more complex habitat quality index for coho salmon proposed earlier by Nickelson (1976) explained 72 percent of the variation in standing crop.

Models **4.04**, **4.05**, and **4.06**--Exclusive of the nine models presented above that are based primarily on three main variables, the rest of the models considered in this category are based on combinations of several different variable types. In a series of reports, Hendrickson and Doonan (1972; **4.04**) and Hendrickson and others (1973b; **4.05**: 1973a; **4.06**) relate standing crops of salmonids in Michigan and Wisconsin streams to numerous variables in all three categories. Although species are not reported, most fish were probably brook trout, brown trout, and rainbow or steelhead trout. As an example of the analyses, Hendrickson and others (1973a) developed complex power function models by transforming the data to logarithms and using multiple regressions (see equation 3). These models predict standing crops of trout for 57 Michigan and Wisconsin streams from channel morphometry, flow, substrate, cover, temperature, and water chemistry. The best model (**4.06**) accounted for 74 percent of the variation in trout biomass. These models indicate that trout populations are greatest in streams with relatively high ground-water discharge, which in turn produces stable base flows and water temperatures as well as higher water hardness, a general index of productivity.

Model 4.07--Platts (1974, 1976; **4.07**) made complete censuses of Dolly Varden, cutthroat trout, rainbow trout, and juvenile chinook salmon in Idaho streams by using explosives, and measured 20 independent variables of all three types along trans-ects. Multiple linear regressions using all the variables accounted for 10-35 percent of the variation in numbers of the four salmonid species; but elevation, stream width, and a pool rating were the most significant variables explaining variation in numbers of all fish (Platts 1974). Platts (1974) found that when land is classified according to geology and geomorphic process, predictable relationships between numbers of fish species and elevation, gradient, and channel width become evident.

Model 4.09--One of the most widely known models predicting stream salmonid standing crop from habitat variables is the habitat quality index (HQI) (Binns 1979, Binns and Eiserman 1979; **4.09**). During initial development of HQI model I, Binns. (1979) measured standing crops of brook trout, brown trout, rainbow trout, and cut-throat trout in 20. Wyoming streams and regressed those standing crops against relative ratings of 10 variables of all three types. The model structure is complicated because each independent variable is rated from 0 (worst) to 4 (best) based on quantitative criteria, and some ratings are multiplied together to form an index. The model also is in the general form of a power function, fitted using multiple linear regression by transforming both dependent and independent variables (the ratings) to logarithms. All these factors make interpretation of the model difficult. Model I accounted for 95 percent of the variation in standing crops at the initial 20 sites, but one stream with a very large standing crop inflated the coefficient of determination, a problem discussed below.

Binns (1979) collected data from 16 more streams to test model I and also combined the two sets of data to develop model II (4.09). Model I explained 59 percent of the variation in standing crop at the 16 new sites, but the relative prediction error may be more significant in judging model accuracy because of the one large datum. The standing crop predicted by model I differed from actual biomass by 38 percent on average. Binns (1979) revised model I by replacing two variables that were time con-suming to measure with one simpler one and by constructing two new indices. Model II, also a complex power function of variable ratings and indices, explained 97 per-cent of the variation in trout biomass for all 36 sites. Finally, Binns (1979) collected data from eight more sites to test model II, which explained 93 percent of the variation and averaged only 12.5 percent prediction error.

Model 4.25--Annear and Conder (1983) tested the HQI for 10 Wyoming streams and found it closely related to the standing crop of stream salmonids ($r^2 = 0.83$, $P<0.05$); but for 5 streams, population estimates were made 1-3 years before habitat measurements. In contrast, White and others (1983; 4.25) applied Binns' (1979) HQI to 30 sections of four Montana streams, but found that actual standing crops of brook trout, brown trout, and rainbow trout were consistently below predicted levels and that the. correlation between HQI and standing crop was low ($r=0.23$). White and others (1983) then calculated separate multiple linear regressions for stream sections in urban areas and nonurban areas and for all stream sections, after transforming HQI variables to logarithms but not rating them. The three models they constructed (for example, 4.25) accounted for 76-95 percent of the variation in standing crop.

Model 4.13--Sekulich (1980; **4.13**) developed several models to predict the biomass of age-0 chinook salmon in pools of several Idaho streams from the number of eggs deposited, channel morphometry, flow, temperature, and biological variables. The. number of eggs deposited was consistently the most important variable in models.

Model 4.14--Fraley and Graham (1981; **4.14**) found that overhead and instream cover, stream order, and substrate accounted for 41 percent of the variation in density of westslope cutthroat trout and bull trout in 134 stream reaches of a Montana watershed. When this regression model was tested by using data from 23 additional reaches in a separate area of Montana, the correlation between observed and predicted trout numbers was 0.63, and the relative prediction error averaged 115 percent.

Models 4.15-4.22--Layher (1983; **4.15-4.22**) developed models to predict standing crops of eight warmwater fish species from variables of all three types by using data collected at 420 sites in Kansas streams.. Independent variables were first converted to suitability index values, a continuous rating from zero to one developed from a separate plot of the standing crop as a function of each independent variable. This technique was developed for use in the U.S. Fish and Wildlife Service (USFWS) habitat evaluation procedures (USFWS 1980, 1981) and effectively standardizes all independent variables to a unitless scale. For each fish species, separate models were developed from data collected by eight different sampling methods. The best models for all species were significant ($P<0.05$) and, except for the green sunfish model (**4.22**), accounted for 90 percent or more of the variation in standing crop. When data were collected, however, to test the models at 50 new sites in Oklahoma, correlations between observed standing crop and that predicted were low and generally not significant. Significant new regressions were developed for most species for the Oklahoma sites and were based on the same suitability indices as for Kansas, but the habitat variables found significant were different. Layher (1983) concluded that attempting to develop such models for large geographic areas is impractical unless species have restricted habitat requirements.

Models 4.23 and 4.24--Scarnecchia (1983) developed the only models we found that estimate production ($g \cdot m^{-2} \cdot year^{-1}$; **4.23**) and biomass (**4.24**) of stream salmonids from habitat. His objective was to construct production models for brook trout, brown trout, rainbow trout, and cutthroat trout in headwater streams in Colorado. He presents a variety of models using two to four variables, such as elevation, width-to-depth ratio, substrate diversity, nitrate, and sulfate. The best models accounted for 60-84 percent of the variation in trout production and 60-75 percent of the variation in biomass.

Models 4.27-4.35--Rabern (1984; **4.27-4.35**) constructed models to predict standing crop of nine warmwater fish species at 75 sites in Georgia rivers from 21 variables of all types. Unlike most investigators who estimated standing crops of fish from mark-recapture or depletion methods by electrofishing, Rabern (1984) used data from surveys with rotenone in rivers to estimate fish abundance. Five models were developed for each species from different subsets of variables and their squares and cross products. Then the optimum number of variables was determined from Mallows' Cp statistic (discussed below), an objective criterion used to arrive at the best model. The best models were all highly significant and accounted for 66-98 percent of the variation in standing crop. When data from two additional river rotenone stations were collected and fish biomass predicted, a number of the models performed poorly, but this was a limited test of the models.

Models 4.36, 4.37, and 4.38--Leathe and Enk (1985) constructed models to predict densities of bull trout (**4.36**), west slope cutthroat trout (**4.37**), and brook trout (**4.38**) from 18 variables of all three types as part of an analysis of the cumulative effects of small hydropower projects in a Montana watershed. All three models incorporated instream cover as an important variable. But in the analysis of cumulative effects of several hydropower installations, the relationship between the density of juvenile bull trout and a substrate condition score proved to be the more important model because it could be linked to the sediment-yield models of Cline and others (1981), a process discussed below.

Several models presented in this category require that more variables be measured to estimate standing crop than do most models in other categories. Many of the variables are also difficult to measure accurately. Fishery managers may therefore find these models prohibitively expensive to use unless variables are easily measured or the data are readily available--or the fishery is so highly valued that costly measurement is justified. We believe these models will be useful only if they apply to the specific situation and geographical region of interest to the manager, a subject discussed below.

Tests of Weighted Usable Area as a Habitat Model

The Instream Flow and Aquatic Systems Group (IFASG) of the USFWS's National Ecology Research Center developed a set of physical-habitat models for stream fish designed for use with the Instream Flow Incremental Methodology (IFIM). The IFIM was originally conceived to estimate changes in fish habitat caused by changes in stream discharge. In this procedure, hydraulic models are used to predict depth, velocity, and substrate within cells of relatively small stream area as functions of flow. The area of each cell is multiplied by the relative preferences (ranging from 0 to 1) of the fish species for the depth, velocity, and substrate found at a given flow. Values for all cells in the stream reach are summed to determine the weighted usable area (WUA). Bovee (1982, 1986) describes ways that joint preference functions for several variables (for example, depth and velocity) can be derived for fish species and indicates that recent IFIM procedures also incorporate cover preference. The reaches of stream with suitable water quality and temperature for each species at each discharge are also predicted by other models.

Users should be aware of several assumptions inherent to the IFIM. The first is that fish respond to average water velocities in each - cell because these are the velocities predicted by the hydraulic models. Stream salmonids are known, however, to choose positions in low-velocity refuges near higher velocities, which maximizes the net energy they gain from feeding on invertebrate drift (Fausch 1984). These sites are often near the streambed and downstream from objects, rather than at the 0.6 depth. Overcoming this assumption greatly increases the complexity of developing preference functions (Bovee 1982). A second assumption is that depth, velocity, and substrate are assumed independent in some preference functions. But these variables are correlated in streams so that fish preference for them should also be related. Bovee (1986) suggests that this assumption poses no problem unless the pattern of dependence for microhabitat use by the fish is different than that for the microhabitat available. A third assumption inherent in using preference functions is that a large amount of suboptimal habitat is equivalent to a smaller amount of optimal habitat. Finally, the IFIM rests on the assumption that the fish population is primarily limited by suitable habitat (temperature and water quality) and microhabitat, not by food, competitors, predators, or fishing mortality. The IFASG is presently working to develop models explicitly incorporating many of these factors.

Models 5.01 and 5.04--An obvious test of WUA is to use it as an independent variable to predict fish standing. crop. Stalnaker (1979; **5.04**) used data from Wesche (1976) in one of the first of these tests and found that WUA accounted for 81 percent of the variation in brown trout biomass in Wyoming streams during late summer. Nehring (1979; **5.01**) found WUA at average discharge to be highly correlated with brown trout biomass in 7 Colorado streams but found no such relation for either brook trout (11 streams) or cutthroat trout (5 streams). Nehring (1979) attributed these low correlations to the preference curves for the latter two species, which the IFASG then considered only fair, whereas those for brown trout were considered good or excellent.

Models 5.02, 5.03, 5.05, and 5.11--In a test similar to those above, Wesche (1980; **5.05**) found that WUA explained 82 percent of the variation in brown trout biomass in four reaches of large Wyoming streams. Nickelson and others (1979) found WUA to be significantly correlated with biomass of juvenile cutthroat trout (**5.02**) and steelhead trout (**5.03**), but it accounted for relatively little of the variation in cutthroat biomass. In contrast, WUA was not correlated with the standing crop of juvenile coho salmon. During a 2-year study of a Michigan stream, Gowan (1,984; **5.11**) found that 83 and 90 percent of the variation in abundance of brook trout and brown trout, respectively, measured bimonthly during the summer was accounted for by the WUA calculated for the average daily flow measured in the previous 2 weeks.

In contrast to these studies, Annear and Conder (1983) found low correlations between WUA and biomass of brown trout and rainbow trout for 10 Wyoming streams (r=0.24 and 0.25, respectively, and neither was significant). But in five streams, the habitat measurements were made 1-3 years later than the population estimates, which casts - serious doubt on the results for these streams.

Models 5.06, 5.07, and 5.08--Orth and Maughan (1982) developed depth, velocity, and substrate preference functions for freckled madtom (**5.06**), central stoneroller (**5.07**), and orangebelly darter (**5.08**) by sampling individual fish in an Oklahoma stream by using electrofishing. Then they calculated WUA for the three species and for juvenile and adult smallmouth bass (using preference functions of Orth and others (1981) for the smallmouth bass) during each season for 2 years in two riffles and two pools. They found no significant correlations between WUA and standing crop of either adult or juvenile smallmouth bass during any season. Similar correlations for freckled madtom, central stoneroller, and orangebelly darter were often significant and were highest during summer when habitat is assumed to be most limiting for stream fish because of low flow.

Models 5.09 and 5.10--Nehring and Anderson (1983, 1984) related standing crop of brown trout **(5.09**) and rainbow trout (**5.10**) to their respective WUA to show how flow limits different salmonid life stages in Colorado rivers. In two rivers, year-class strength was positively correlated with WUA during peak runoff periods, a result similar to their analysis described above for flows. Nehring and Anderson (1984) also found that the maximum biomass of brown trout age 2+ and older was highly correlated with the maximum WUA in 10 rivers for which 1-8 years of data were available. Most rivers had catch-and-release regulations or low bag limits.

Models 5.12, 5.13, and 5.14--Loar and others (1985) tested how well WUA predicted standing crops of brown trout (**5.12, 5.13**) and rainbow trout (**5.14**) in southern Appalachian streams. For each species, they correlated standing crop of each age class to WUA and to percentage of usable area (WUA divided by total stream area) for each life stage. They also calculated instantaneous correlations, those using flows measured when populations were estimated, and minimum habitat correlations, those based on the historical mean monthly flow producing the minimum WUA for each life stage.

Even though Loar and others (1985) calculated a matrix of all correlations, we consider as biologically significant only those instantaneous correlations calculated from data for the same life stage (for example, age-0 abundance vs. fry WUA) and only those minimum habitat correlations calculated using WUA for the same or a previous life stage (for example, adult abundance vs. adult, juvenile, fry, incubation, or spawning WUA). We reasoned that minimum WUA may be relevant to succeeding life stages, but not to preceding ones.

Loar and others (1985) found that analysis of minimum habitat for brown trout produced more significant correlations than did the instantaneous correlations. Standing crops of rainbow trout showed little relation to habitat in either analysis, however. They suspected that competition with brown trout might limit rainbow trout in sympatry, so they analyzed the allopatric rainbow trout populations separately and found several significant correlations with WUA.

In addition to the IFIM, the USFWS has also developed habitat evaluation procedures (USFWS 1980, 1981) to predict habitat quality units from habitat suitability index (HSI) models. A number of HSI models for both coldwater and warmwater stream and river fish were recently tested by investigators to determine whether model output was related to standing crop (Terrell 1984). We chose not to review these tests because they are assembled in a readily available volume including a review and summary of the work by Terrell and Nickum (1984).

Assessing Model Quality and Important Habitat Variables

Levins (1966) outlined three desirable attributes of models: realism, precision, and generality. He believed that, at most, two of the three attributes can be attained in biological models. Ideal models for standing crops of stream fish would incorporate all the important functional attributes of fish population response to habitat (that is, be realistic); account for a large percentage of the variation in standing crop and give repeatable results (that is, be precise); and be based on many years of data collected from a broad geographic area (that is, have wide generality) so that 50 or more degrees of freedom remain after fitting model parameters.

We attempted to assess model precision and generality by using simple criteria available for most of the models we reviewed: coefficient of determination, sample size, and degrees of freedom. Of the 98 models we reviewed where sample size was reported, 39 were developed from data sets of more than 20 observations (fig. 1), but only 18 of these models accounted for 75 percent or more of the variation in standing crop. Conversely, 40 of the 59 models calculated from fewer than 20 samples had coefficients of determination of 0.75 or greater. We conclude that most relatively precise models stem from data collected over relatively short periods (often only one season of one year), or over relatively small geographic areas (often a single stream or watershed), or both, and thus lack generality.

We also calculated the degrees of freedom (sample size minus the number of regression coefficients fitted, including the intercept) for the 95 models where the information was available, because degrees of freedom is an even better indicator of model generality than sample size. Only 31 of the models had more than 20 degrees of freedom (fig. 2), and only 15 of these accounted for more than 75 percent of the variation in standing crop. In contrast, 43 of the 64 models with fewer than 20 degrees of freedom accounted for 75 percent or more of the variation, again indicating that relatively precise models often lack generality.

Even though a model is precise, it is not necessarily realistic or accurate. Model accuracy can be tested only by repeating the estimates of model coefficients independent of the original means. Several investigators attempted such tests of their models by collecting additional data, as we discuss below.

When researchers initially construct a model, they usually question which habitat variables the standing crop of stream fish should be closely related to. When we grouped models by sample size, coefficient of determination, and the five categories of variables, we found that the majority of models with the larger sample sizes (>20) and greater coefficients of determination (>0.50) used a combination of variable types (fig. 3). We took this another step and analyzed the variables most frequently found significantly related to standing crop in the 85 models we reviewed, excluding the 14 WUA tests (table 10, appendix). Although most variables were used in only

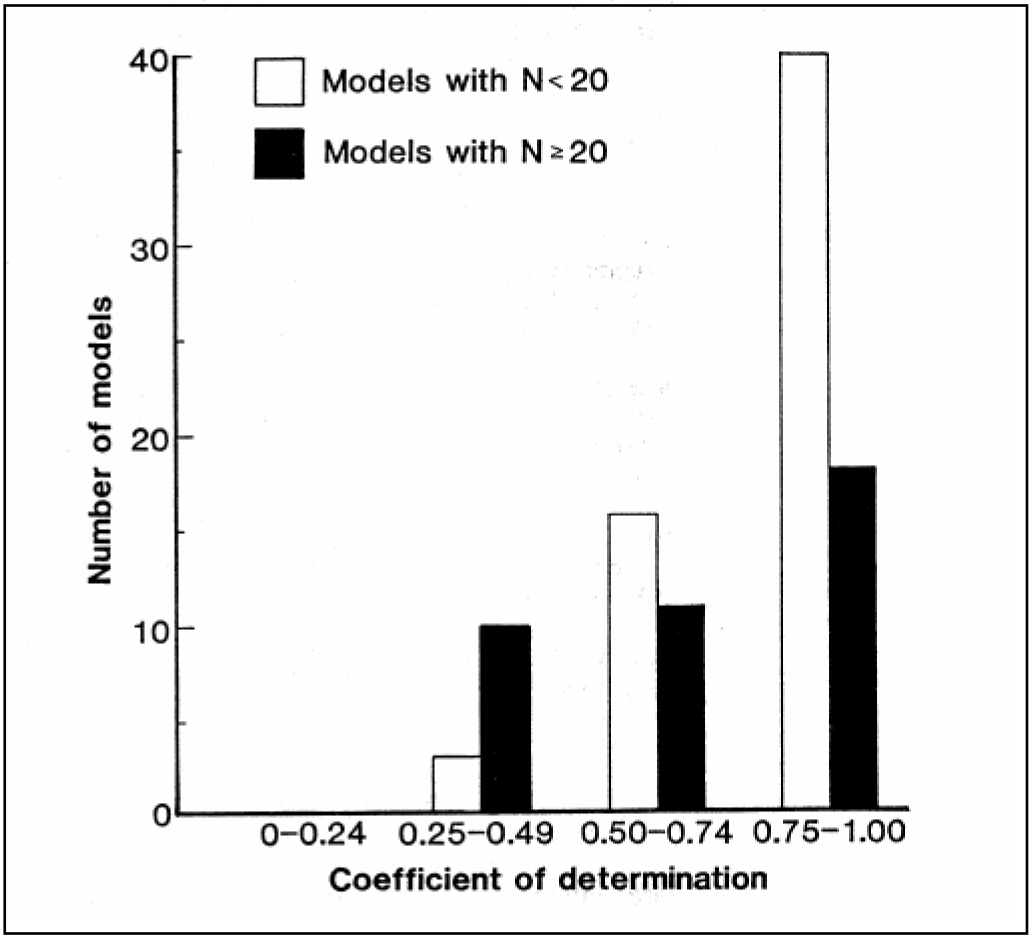

Figure 1-- The reviewed models are divided into groups by sample size and by the coefficient of determination. Only 98 models are shown because the sample size was not reported for 1 model.

one or two models, seven emerged as most often being significant when we grouped similar variables together. Measures of instream, overhead cover were most frequently significant (22 models) followed by depth (20 models), alkalinity/hardness/conductivity (15 models), mean stream flow (14 models), width (14 models), surface area (12 models), and dissolved oxygen (11 models). More than one variable of a given type sometimes occurred in the same model. Each of these variables was also found significant in one or more of the models with greater precision and generality (r^2>0.50 and 20 or more degrees of freedom, table 10). This analysis is biased, however, because investigators (often used data at hand or evaluated easily measured variables. The variety of ways similar habitat variables are measured (table 9) has spurred recent calls for standardization (Mullan 1983, Platts 1983, Wesche 1983).

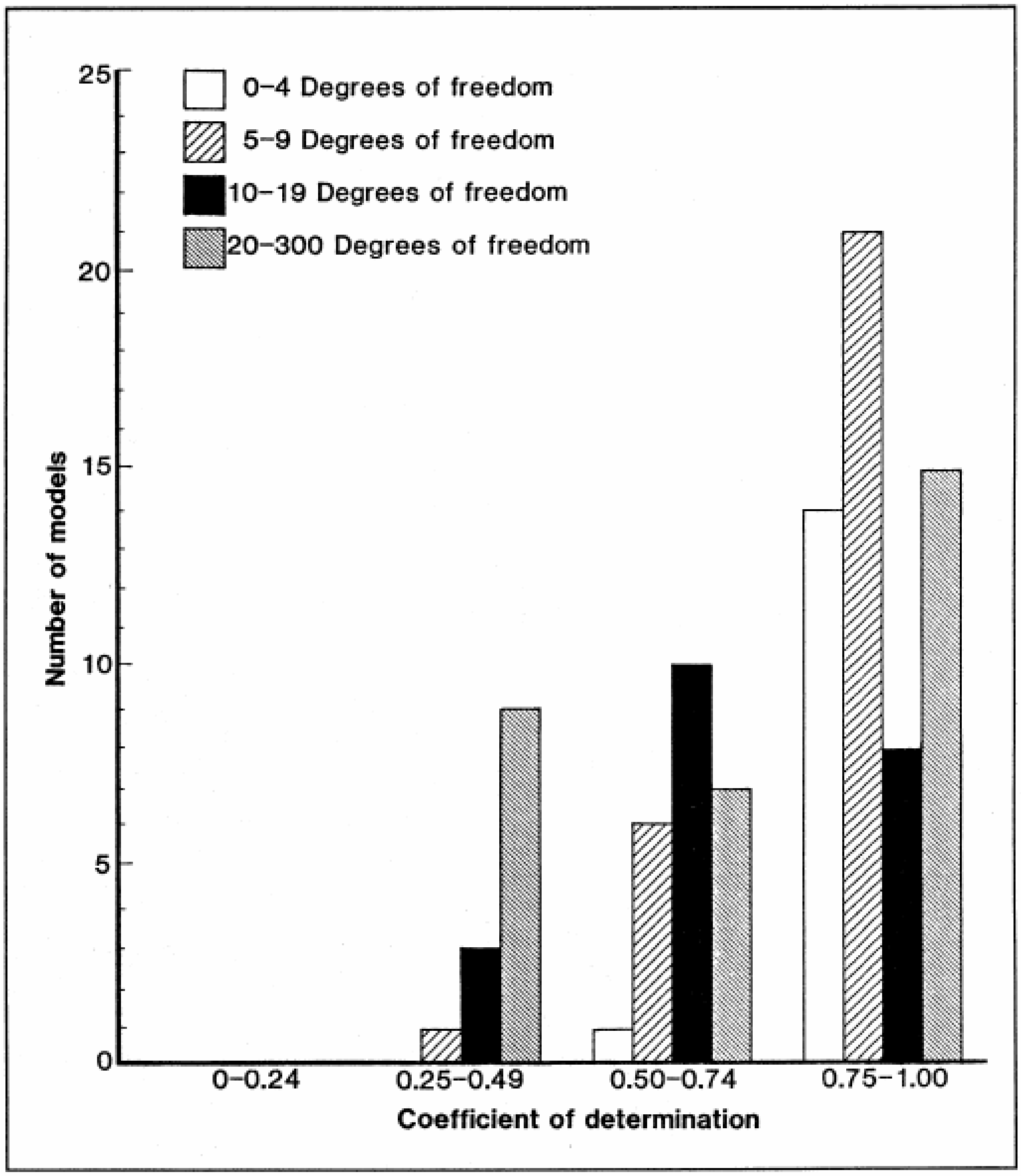

Figure 2--The reviewed models are divided into groups by degrees of freedom and by the coefficient of determination. Only 95 models are shown because the information needed to determine degrees of freedom was not reported for 4 models.

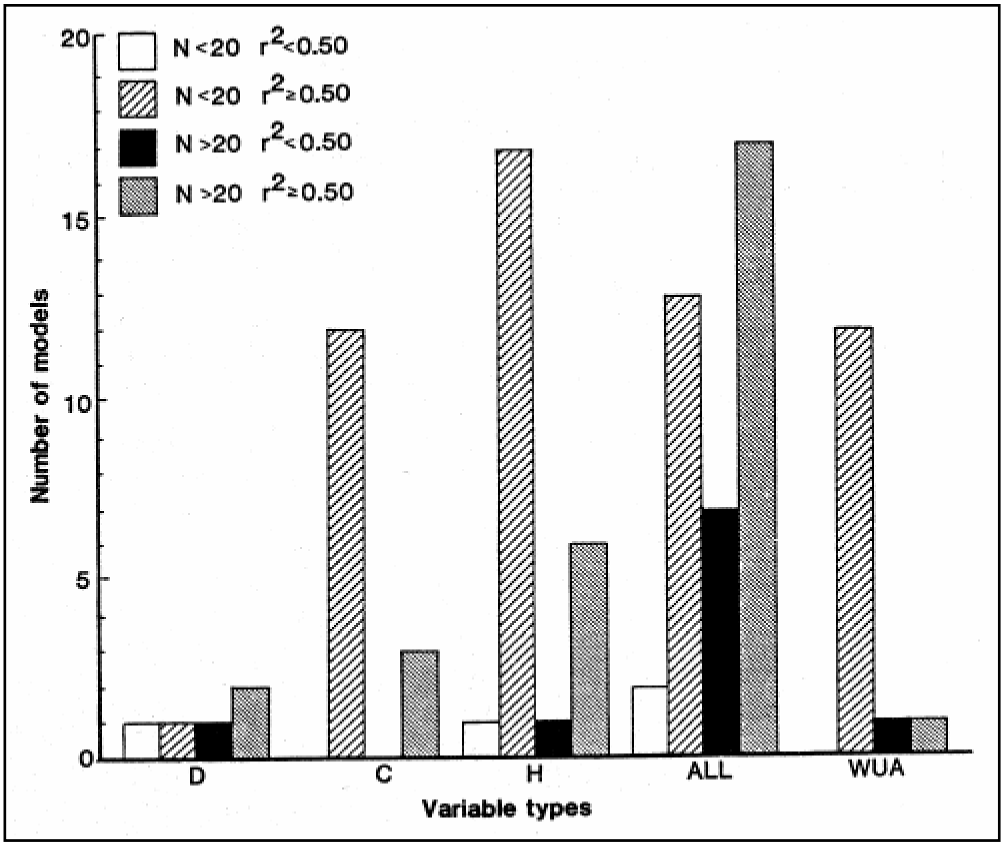

Figure 3- The reviewed models are divided into groups by type of independent variables and by sample size and the coefficient of determination,. Categories of variables are D = drainage basin variables; C = channel morphometry and flow variables; H = habitat-structure, biological, physical, and chemical variables; ALL = combination of the three preceding variable types; and WUA = tests of weighted usable area. Only 98 models are shown because the sample size was not reported for 1 model. .

Hall and Knight (1981) reviewed literature on natural variability of stream salmonid populations and classified factors affecting fish abundance as either physical (streamflow and physical habitat) or biological (food abundance, predation, and movement and migration). They found, as we did, that physical habitat characteristics, particularly the many forms of cover, are most closely related to salmonid abundance, and they suggested that these should be the first variables to include in habitat assessment .

Improving Habitat Models

While reviewing the 55 investigations presenting stream-fish habitat models (tables 1-5), we found that sound sampling or statistical procedures were often minimized or overlooked during model development. A full discussion of sampling and statistical inference is beyond our scope, but the investigator clearly must first define the population of sites or streams of interest. Then a proper sample can be drawn, the data analyzed, and rigorous inductive inference made from this sample to the defined population. If data are collected, however, in only a few years or from only a few streams, strong inference (Platt 1968) cannot be made about the importance of habitat variables across years or in areas beyond the defined population. Hall and Knight (1981) report that temporal and spatial variation in salmonid abundance may be as extreme as several orders of magnitude and that even moderate annual variation can mask significant changes in the aquatic environment.

A full discussion of the best ways to build linear regression models, the type most frequently developed to date, is also beyond the scope of this paper. We found Neter and Wasserman (1974), Weisberg (1980), and Draper and Smith (1981) to be excellent guides for our use. Prospective model builders are strongly advised to seek a knowledgeable statistician during project planning. If these sources of information are used, investigators will be able to select proper procedures to assess colinearity among independent variables, estimate model parameters (the regression coefficients), and analyze residuals to test model assumptions and fit. When fitting regressions to transformed exponential and power functions (see equations 2 and 3), for instance, modelers must first determine whether errors in the dependent variable are additive or multiplicative to ensure that these transformations are valid before using them. Here we address other problems we found most frequently in model development and testing, such as inadequate sample size, error in measuring independent variables, choosing the best model, testing models, and using models to predict standing crop. We also address unrealistic assumptions usually made when the standing crop of stream fish is estimated and when major biological assumptions are made in most models.

Sample Size

The most common problem among the models we reviewed was inadequate sample size. Data were frequently measured at too few locations for too few dates (often $N<20$; see fig. 1) to encompass the range of variation in the fish populations or habitat variables that one would expect in even a small area over a relatively short period. This problem was frequently exacerbated by considering too many variables for the relatively small sample size, which resulted in small degrees of freedom (fig. 2); for example, when most of the degrees of freedom are used to estimate regression coefficients, the resulting model cannot be expected to accurately predict standing crops under different conditions.

In fairness to many investigators, the relationships they calculated were intended to describe only the data they measured. But once a regression or correlation is published, the danger always exists that another researcher will use it for prediction without first critically evaluating and testing the model to determine whether it applies under the new conditions.

Error in Measuring Habitat Variables

A second problem common among .models was that the procedures used to fit linear regression models assume that the independent habitat variables are measured without error (Neter and Wasserman 1974, Sokal and Rohlf 1981). Because this assumption is often violated when stream habitat is measured, variance in independent variables is an important consideration when model parameters are estimated because these estimates may be biased. Weisberg (1980) suggests assessing this problem by conducting sensitivity analysis to determine how much the model slope and intercept would change if the habitat variables were changed by an amount reflecting measurement error. If the error can be measured or even estimated, a better method is to calculate the resulting bias in slope by using the estimator in Snedecor and Cochran (1967) to determine whether the error is worth considering.

Platts (1981), Leathe and Graham (1983), Platts and others (1983), and Leathe and others (1985) are the only investigators we found who evaluated the error in measurement of habitat variables. Platts (1981) and Platts and others (1983) made repeated measurements of habitat over 7 years in 56 streams in Idaho, Nevada, and Utah. They analyzed data precision by calculating 95-percent confidence intervals and expressing them as percentages of the mean value. They also assessed accuracy of this mean subjectively by observations and photos at specific points to determine whether measurements by different observers over time reflected actual changes in habitat variables. Not surprisingly, variables measured with excellent precision (half-width of the confidence interval <5 percent of the mean) were those that could be precisely defined for an observer and measured with an instrument, such as width and depth of the stream. Variables judged visually, such as percentage of boulder substrate, had larger confidence intervals and low precision of measurement. They found that accuracy in measuring habitat is hampered by bias caused by different observers and by natural change in habitat features over time.

Leathe and Graham (1983) and Leathe and others (1985) calculated the relative percentages of differences in habitat measurements made by different crews in the same sections of several Montana streams. Again, quantitative measurements (for example, width and depth) were least variable, and qualitative ones (for example, pool class and percentage of riffle-run) were most variable.

Choosing the Best Model

The third common problem investigators face is how to choose the best model. Unfortunately, no automatic procedure exists for model selection because model usefulness depends partially on the investigator's biological knowledge about how the habitat variables should be related and also on whether model predictions are precise enough for the intended use. Certain statistical procedures, especially in multiple regression, can aid in choosing the optimum model. In the past, investigators usually calculated such models from stepwise computer algorithms that generated one best model. But statisticians agree this method is unsuitable because the order that additional variables enter or leave the model has no functional significance (Johnson 1981, Weisberg 1980). It is better to calculate all possible models by using "all subsets" regression and to choose the best one for a given number of independent variables (for example, the best regression with three independent variables) by using an objective criterion such as Mallows' Cp statistic, which minimizes the mean square error of prediction (Weisberg 1980). Among the models we reviewed, only Rabern (1984) chose subsets based on this criterion, although White and others (1983) and Lanka (1985) chose models based on R^2 adjusted for degrees of freedom, a related and useful criterion.

Another poor practice is choosing models based solely on the coefficient of determination, as we did in our study for lack of a better criterion. This measure of association can be inflated by one sample of large value or be deflated if all data are closely spaced (Neter and Wasserman 1974). In multiple regression, R2 increases as variables are added, so the largest model will always be chosen if this is the sole criterion, rather than the adjusted R2 mentioned above.

An important consideration in choosing the best model is the ease and expense of measuring habitat variables. Several investigators reported alternative models that were based on how difficult or costly variables were to measure (Marshall 1985, Scarnecchia 1983).

Testing Models

A fourth problem in model development is that relatively few investigators attempted to test or validate their models to determine whether they were accurate at another time or place. Exclusive of the recent tests of WUA as a habitat model (table 5), only Binns (1979), Nickelson and others (1979), Eifert and Wesche (1982), Fraley and Graham (1981), Annear and Conder (1983), Layher (1983), White and others (1983), Rabern (1984), Lanka (1985), and McClendon and Rabeni (1985) undertook tests of their own models or those of others. These studies provide several examples of models that have been tested relatively extensively. Nickelson and others (1979) calculated 95-percent prediction intervals for models of three salmonid species (**4.10, 4.11,4.12**) and then tested the models by determining the percentage of new observations falling within the prediction intervals. If the model truly reflects conditions at the new sites, 95 percent of the new samples would be expected to fall within this interval, but Nickelson and others (1979) found that only 48, 57, and 88 percent of the 20-318 new observations did so for the three models (see description of models above, and table 4).

Binns (1979) tested his initial Hal model with new data, then developed a second model (4.09) and tested that with a third data set. The tests indicated that the second model is relatively precise and has wide generality in Wyoming. But we suspect the models of both Binns (1979) and Nickelson and others (1979) may sacrifice realism because both combine habitat variables in such complex ways that assessing whether they accurately reflect the functional response of fish to habitat is difficult. Eifert and Wesche (1982), White and others (1983), and Annear and Conder (1983) also conducted further tests of the HQI Wyoming and Montana with mixed results (see model descriptions above).

Weighted usable area has been tested by several investigators for a number of species, but most of the tests were made with relatively small sample sizes (table 5). These tests nevertheless have helped define further data needs for habitat suitability criteria (Bovee 1986) used in the IFIM procedures. Fraley and Graham (1981), Layher (1983), Lanka (1985), and McClendon and Rabeni (1985) also collected data at 10 or more new sites to test their models.

Using Models to Predict Standing Crop

A fifth problem occurs because biologists usually want to use habitat models to predict what will happen at another place .or in the future when conditions change. Unfortunately, the existence of a significant regression does not assure that useful predictions can be made from it; this depends on several factors, one being the width of the prediction interval. Yet few investigators report this interval or supply the standard error of regression ($Sy|x$) and other values needed to calculate it.

To minimize misuse of models for prediction, investigators should supply readers with the ranges of values measured for each habitat variable during model development (for example, see Rabern 1984 and Lanka and others 1987) and caution not to extrapolate outside these ranges. Models also pertain to the geographic area where data were collected and may predict poorly even in adjacent areas, as Layher (1983) found when he developed models in Kansas and tested them in Oklahoma.

Most important, when data are observational rather than experimental, investigators must be careful of making statements about data other than those observed (Weisberg, 1980); that is, making the inductive leap. We found that using most models to predict standing crop would be a risky inductive leap because habitat variables were not experimentally controlled or manipulated by the investigators. Without experimental manipulation of habitat, changes in the habitat variables cannot be considered to have caused the observed changes in the standing crop of fish. Instead, the habitat variables found to be significantly related to standing crop may be correlated with other unmeasured variables directly affecting fish populations. Thus, when using observational data to build models, the modeler must assume that the ecosystem will behave the same way when predictions are made at a different time or place.

Only Hunt (1971), Kraft (1972), and Randolph and White (1984) were able to manipulate, habitat variables and measure the response; even then, most variables were not strictly controlled. But many habitat variables, .such as elevation and nearly all other drainage basin variables, cannot be manipulated. The link between these variables and fish production can be established only through careful development and testing of many models in several regions.

In search of the. biological significance of their models, some investigators suggest mechanisms whereby the variables found significant could control standing crop. Although this procedure is a necessary part of model building (Weisberg 1980) and may provide hypotheses about the controlling mechanisms, the only true test of the biological significance of habitat variables is repeated experimentation. To draw conclusions, the researcher must actually manipulate habitat variables and measure the responses.

Estimating Standing Crop of Stream Fish

The sixth problem is that most investigators estimated standing crop of fish, the dependent variable in most models, by using electrofishing to determine two-pass mark-recapture or removal. estimates. Recent work indicates that the Petersen, Schnabel, Leslie, and Seber-LeCren estimators commonly used often yield poor population estimates because they make unrealistic assumptions, especially about equal catchability of different sizes of fish during different sampling occasions, and of marked versus unmarked ,fish (Otis and others 1978, White and others 1982). White and others (1982) present a readable manual describing newer maximum-likelihood estimators that explicitly account for unequal catchability and a microcomputer program (CAPTURE) that is available to calculate the estimates.

An important assumption common to all the models is that the population is closed when the estimate is made. Unfortunately, blocking stream sections for long periods to ensure closure is difficult. Most mark-recapture models presented by White and others (1982) also require the fish to be individually marked, or at least batch marked on each capture occasion, which may be too time consuming, costly, or harmful for some fish. Removal estimators appear more suitable for stream-fish populations because stream sections can usually be blocked with nets for one day while the fish are removed by successive electrofishing passes. But experience of the senior author indicates that four or more removal passes are often required to satisfy model assumptions and to achieve accurate estimates of fish populations even in small streams. Repeated electrofishing unfortunately causes added mortality of young fish and may affect growth of adult fish (Gatzand others 1986). Some investigators (for example, Platts 1974, and Rabern 1984) used other methods such as explosives or rotenone to sample fish. Although these methods are less size selective than electrofishing, they are destructive and, we suspect, are biased to an unknown degree.

Major Biological Assumptions

A major biological assumption common to all models is that the fish population is limited by the set of habitat variables included in the model. The last problem is that few investigators addressed whether fishing, interspecific competition (Li and others 1984, Loar and others 1985), or predation might be limiting the standing crop below what the environment could support. Clearly, accurate models cannot be constructed unless these factors are eliminated or accounted for.

How Habitat Models Are Used

Habitat models are presently used in five main ways in fishery management. First and most obvious is to predict standing crops of stream fish under present conditions, perhaps for general inventory or planning. But relatively few biologists use habitat models for this purpose, probably because, as White (1983) suggests, it is often easier to perform the population estimates than to measure the habitat variables, or because fish biologists traditionally inventory fish populations to gather data on size and age.

A second reason investigators construct such models is that significant independent variables should point to fundamental mechanisms that control standing crop and further the process of developing a theoretical understanding of relations between stream habitat and fish populations. Thus, because Nickelson and others (1979) found that pool volume alone accounted for 94 percent of the variation in juvenile coho salmon biomass in Oregon streams, deep pools are inferred to be critical rearing habitat for coho. But linear regression implies no cause-effect relationship, as discussed above, so pools of different volumes would have to be created to determine whether this factor controls coho biomass.

A third use of models is in assessing the habitat quality of a specific stream reach by determining which habitat variables contribute to a low standing crop; that is, by asking, "What is wrong with the habitat in this stream?" Managers in Wyoming, for instance, might use Binns (1979) Hal to assess habitat by determining which variables have low ratings and also have the greatest effect on predicted standing crop. But some offending variables cannot be improved by management, a point discussed below.

A fourth common use is to predict changes in standing crop given proposed detrimental (removal of water, channelization) or favorable (habitat enhancement) changes in habitat. For example, the IFIM is used to predict changes in habitat and, in turn, fish populations, given changes in flow regime or channel morphometry (Bovee 1982) or improved habitat (Hardin and Bovee 1983). Binns' (1979) HQI has also been used to predict reductions in standing crops of stream salmonids with proposed removal of water (Binns 1982). Stuber (1985) used the HQI to predict increases in salmonid standing crop after habitat improvement in several northern Colorado streams. The predictions were made soon after the work was completed, even though Stuber expected the fish populations to take several years to reach maximum abundance or carrying capacity.

In response to the Forest and Rangeland Renewable Resource Planning Act of 1974 and the National Forest Management Act of 1976,- the USDA Forest Service is developing and using models in a fifth way: to predict changes in standing crops of stream fish caused by the cumulative effects of different forest management alternatives. Heller and others (1983) present such an analysis for the Siuslaw National Forest in Oregon. It was used to compare the economic value of anadromous fish with that of timber resources and thereby assess management alternatives. Stowell and others (1983) and Leathe and Enk (1985) also linked sediment yield models of Cline and others (1981) with models predicting stream fish from habitat to predict changes in standing crops under different timber harvesting practices in each watershed. We suspect that the statistical ramifications of linking two models, both having associated prediction errors, need further thought by investigators attempting cumulative-effects modeling.

A sixth and final use of models is to indirectly assess fishing mortality. Stuber (1985) assumed that after habitat improvement, trout biomass in three streams should increase to the level predicted by the Hal (Binns 1982). Stuber proposes that in streams where this does not occur, fishing mortality is reducing standing crop below carrying capacity, and special regulations maybe in order. Stuber (1985) suggests that this assessment is less expensive than creel census and would allow managers time to implement conservative measures in regulating harvest

Nehring and Anderson (1984) used the ratio of maximum measured trout biomass per WUA, in 10 Colorado rivers with zero or low bag limits, as a measure of carrying capacity .For overexploited river reaches, they propose multiplying this standard by the measured WUA to estimate potential fish biomass attainable under catch-and-release regulations. Managers using models predicting stream fish from habitat to assess fishing mortality should be aware that other factors besides fishing mortality limit fish populations below carrying capacity.

Because none of the models described in this section were developed through manipulative experiments, each of the uses described involves a risky inductive leap, often beyond the defined population of streams to which inferences are valid. This induction may lead to inaccurate predictions and poor management decisions. To avoid this problem, experimentation is essential to develop the underlying theory on which to base accurate predictive models.

Making Models Useful for Fishery Managers

Fishery managers working for State and Federal natural resource agencies are frequently asked to help examine costs and benefits to all resources of alternative management practices. Forest Service fish and wildlife biologists, for example, help plan timber management for optimum use of all natural resources on forest lands. The decline in aquatic habitat caused by timber management, agriculture, livestock grazing, energy development, and recreation is forcing land managers to develop models for tradeoff analysis. When the effects of many watershed disturbances (for example, sediment from erosion being transported to downstream reaches and accumulating through time) combine to degrade aquatic habitat, models must be developed to account for these cumulative effects.

A model must meet several requirements to be useful for analysis of management alternatives. First, the model must include variables that can be affected by management. Because elevation, for instance, cannot be affected by different range management practices, it is an insensitive variable in these analyses, even though it may be used as a covariate because it has important effects on standing crop of stream fish in mountainous regions. In contrast, a measure of eroding banks would be a useful variable in a model designed to assess range management practices.

Second, the region for which the model accurately predicts standing crop must be known. One approach that holds promise for increasing the precision of model prediction is to first delineate ecoregions or land-water ecosystems encompassing areas of homogeneous climate, geology, landform, and soils, and then develop models applying to these prescribed land areas. Hierarchical classifications of both land-aquatic ecosystems (Lotspeich 1980, Lotspeich and Platts 1982, Platts 1974) and ecoregions (Bailey 1980, 1984; Hughes and Omernik 1981; Omemik and Gallant 1986; Omernik and others 1981) have been promoted by investigators of the Forest Service and the U.S. Environmental Protection Agency to simplify natural resource management. Larsen and others (1986), Hawkes and others (1986), and Hughes and others (1987) have investigated relations between attributes of fish communities and ecoregions. The Forest Service is currently funding research in several ecoregions of North America to determine whether streams draining lands formed by similar processes have similar habitat and, in turn, similar standing crops or production of fish.

Present approaches to determining the cumulative effects over time of various management activities on fish populations involve .linking a model predicting fish standing crop from habitat variables to one predicting these same habitat variables from land management practices. As previously described, only a few investigators have done this (Heller and others 1983, Leathe and Enk 1985, Stowell and others 1983), but more work is needed to determine the statistical problems of linking two such models.

Managers of fish habitat also need to compare present fish standing crops, given management activities, with those attainable under undisturbed conditions and in land types having no undisturbed areas. To do this, Parsons and others (1981) made a model of fish habitat as a function of four geomorphic variables for the Siuslaw National Forest in Oregon and showed statistically that their model was applicable to lands with no undisturbed areas. If investigators can determine that both this type of model and one predicting fish biomass from the same habitat variables apply over a certain array of land types, then the two could theoretically be coupled to predict "natural" fish biomass from geomorphic variables.

Drawing conclusions about the future of. models predicting stream-fish standing crop from habitat is difficult, given the diverse array of models we reviewed and the rate new models are being developed. One speculation seems warranted, however: when faced with managing a highly valued fishery resource in a circumscribed system, such as a resident salmonid population below a hydroelectric dam near an urban area, a fishery biologist can afford to gather detailed information about factors limiting the population and will likely be successful in developing a relatively precise model based on a few variables. But the model may apply only to that specific situation and thus will have little generality. At the other extreme, when attempting to manage a diffuse fishery resource of low perceived value, such as a nongame cyprinid occurring statewide, the biologist will likely develop a model based on more variables that has wider generality but relatively low precision. For the latter case, and many that fall in between, we propose that model precision could be improved by stratifying lands into homogeneous ecoregions.

To conclude, we again stress the need for careful experiments designed to test hypotheses about mechanisms underlying the response of fish populations to habitat. For habitat variables that cannot be manipulated, equally rigorous cycles of statistically sound model building and testing are needed in various ecoregions to determine mechanisms. The fruits of these two approaches will be an underlying theory on which to base sound fishery and habitat management.

Acknowledgments

We thank the many people who sent us publications describing models, or aided our search for models and other information, including Bob Behnke, Ted Bjornn, Ken Bovee, Paul Brouha, Mike Enk, Wayne Hubert, Bruce Menzel, Charlie Rabeni, Tony Rabern, Jim Terrell, Pat Slaney, Tom Wesche, Bob White, and Ray White. Carl Armour, Mark Bain, Bob Behnke, Paul Brouha, Dave Bowden, Mike Clady, Ian Fletcher, Karen Galat, Dick Holthausen, Dave Miller, Eric Rexstad, Clare Stalnaker, Tom Wesche, and Ray White made helpful comments on earlier drafts. We especially thank David R. Anderson for a critical and insightful review that greatly improved the manuscript and shaped its character. We are grateful to Karen Esterholdt for judicious editing and to Fred Everest for making the publication of this manuscript possible. Funding to produce the manuscript was provided by the USDA Forest Service, Wildlife and Fishery Ecology Unit, and by the Pacific Northwest Research Station, RWU-4202, to publish it.

Literature Citations

Allen, K. Radway. 1951. The Horokiwi stream: a study of a trout population. Fish. Bull. 10. Wellington, New Zealand: New Zealand Marine Department. 237 p.

Annear, Thomas C.; Conder, Allen L. 1983. Evaluation of instream flow methods for use in Wyoming. Cheyenne, WY: U.S. Department of the Interior, Bureau of Land Management; completion report; contract Y A-512-CT9-226. 248 p.

Bailey, A.G. 1980. Descriptions of the ecoregions of the United States. Misc. Publ. 1391. Washington, DC: U.S. Department of Agriculture. 77 p. and map.

Bailey, Robert G. 1984. Testing an ecosystem regionalization. Journal of Environmental Management. 19: 239-248.

Barber, W.E.; Oswood, M.E.; Deschermeier, Stephen J. 1981a. Validation of two habitat fish stream survey techniques: the area and transect methods. Ketchikan, AK: U.S. Department of Agriculture, Forest Service; final report; contract 53-0109-0-00054. 64 p.

Barber, Willard E.; Oswood, Mark E.; Deschermeier, Stephen J. 1981b. Validation of two fish habitat survey methods in southeast Alaska. In: Armantrout, N.B., ed. Acquisition and utilization of aquatic habitat inventory information. Bethesda, MD: Western Division, American Fisheries Society: 225-231.

Binns, N. Allen. 1979. A habitat quality index for Wyoming trout streams. Monogr. Ser.,Fish. Res. Rep. 2. Cheyenne, WY: Wyoming Game and Fish Department. 75 p.

Binns, N. Allen. 1982. Habitat quality index procedures manual. Cheyenne, WY: Wyoming Game and Fish Department. 209 p.

Binns, N.A.; Eiserman, F .M. 1979. Quantification of fluvial trout habitat in Wyoming. Transactions of the American Fisheries Society. 108: 215-228.

Bovee, K.D. 1982. A guide to stream habitat analysis using the instream flow incremental methodology. Instream Flow Inf. Pap. 12, FWS/OBS-82126. Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service. 248 p.

Bovee, K.D. 1986. Development and evaluation of habitat suitability criteria for use in the instream flow incremental methodology. Instream Flow Info Pap. 21, Biol. Rep. 86(7). Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service. 235 p.

Brett, J.R. 1951. A study of the Skeena River climatological conditions with particular reference to their significance in sockeye production. Journal of the Fisheries Research Board of Canada. 8: 178-187.

Bulkley, R.V.; Benson, N.G. 1962. Predicting year-class abundance of Yellowstone Lake cutthroat trout. Res. Rep. 59. Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service. 21 p.

Burns, James W. 1971. The carrying capacity for juvenile salmonids in some northern California streams. California Fish and Game. 57: 44-57.

Burton, R.A.; Wesche, T .A. 1974. Relationship of duration of flows and selected watershed parameters to the standing crop estimates of trout populations. Water Resour. Ser. 52. Laramie, WY: Water Resources Research Institute, University of Wyoming. 86 p.

Chisholm, Ian M.; Hubert, Wayne A. 1986. Influence of stream gradient on standing stock of brook trout in the Snowy Range, Wyoming. Northwest Science. 60: 137-139.

Chow, V.T., ed. 1964. Handbook of applied hydrology. New York: McGraw-Hill. [Chapters paginated individually].

Cline, Richard; Cole, Gene; Megahan, Walt; Patten, Rick; Potyondy, John. 1981. Guide for predicting sediment yields from forested watersheds. Ogden, UT: U.S. Department of Agriculture, Forest Service, Northern and Intermountain Regions. 48 p. and appendices.

Draiper, Norman R.; Smith, Harry. 1981. Applied regression analysis. 2d ed. New York: J. Wiley and Sons. 709 p.

Drummond, Robert A. 1965. Reproduction and harvest of cutthroat trout in Trappers Lake, Colorado. Fort Collins, CO: Colorado State University. 68 p. M.S. thesis.

Duff, D.A.; Cooper, J.L. 1978. Techniques for conducting stream habitat surveys on national resource land. Tech. Note 83. Salt Lake City, UT: U.S. Department of the Interior, Bureau of Land Management. 73 p.

Eifert, W.H.; Wesche, T.A. 1982. Evaluation of the stream reach inventory and channel stability index for instream habitat analysis. Water Resour. Ser. 82. Laramie, WY: Water Resources Research Institute, University of Wyoming. 106 p.

Enk, Michael D. 1977. Instream overhead bank cover and trout abundance in two Michigan streams. East Lansing, MI: Michigan State University. 127 p. M.S. thesis.

Fausch, Kurt D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology. 62: 441-451.

Fraley, John J.; Graham, Patrick J. 1981. Physical habitat, geologic bedrock types and trout densities in tributaries of the Flathead River drainage, Montana. In: Armantrout, N.B., ed. Acquisition and utilization of aquatic habitat inventory information. Bethesda, MD: Western Division, American Fisheries Society: 178-185.

Frenette, M.; Caron, M.; Julien, P.; Gibson, R.J. 1984. Interaction entre le débit et les populations de tacons *(Salmo salar)* de la rivière Matamec, Québec. Canadian Journal of Fisheries and Aquatic Sciences. 41: 954-963. In French.

Gatz, A. John, Jr.; Loar, James M.; Cada, Glenn F. 1986. Effects of repeated electrofishing on instantaneous growth of trout. North American Journal of Fisheries Management. 6: 176-182.

Gordon, D.J.; MacCrimmon, H.R. 1982. Juvenile salmonid production in a Lake Erie nursery stream. Journal of Fish Biology. 21: 455-473.

Gowan, Charles. 1984. The impacts of irrigation water withdrawals on brown trout *(Salmo trutta)* and two species of benthic macroinvertebrates in a typical southern Michigan stream. East Lansing, MI: Michigan State University. 127 p. M.S. thesis.

Hall, J.D.; Knight, N.J. 1981. Natural variation in abundance of salmonid populations in streams and its implications for design of impact studies. EPA-600/S3-81-021. Corvallis, OR: U.S. Environmental Protection Agency. 85 p.

Hardin, Timothy S.; Bovee, Ken D. 1983. Use of the instream flow incremental methodology to design habitat improvement features: St. Vrain rehabilitation study. Proceedings of the stream mechanics workshop; 1983 June 16; Fort Collins, CO. Fort Collins, CO: U.S. Department of Agriculture, Soil Conservation Service. 29 p.

Harshbarger, T.J.; Bhattacharyya, H. 1981. An application of factor analysis in an aquatic habitat study. In: Capen, D.E., ed. The use of multivariate statistics in studies of wildlife habitat. Gen. Tech. Rep. RM-87. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 180-184.

Hawkes, Clifford L.; Miller, David L.; Layher, William G. 1986. Fish ecoregions of Kansas: stream fish assemblage patterns and associated environmental correlates. Environmental Biology of Fishes. 17: 267-279.

Hawkins, C.P.; Murphy, M.L.; Anderson, N.H.; Wllzbach, M.A. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. Canadian Journal of Fisheries and Aquatic Sciences. 40: 1173-1185.

Heller, David A.; Maxwell, James R.; Parsons, Mit. 1983. Modeling the effects of forest management on salmonid habitat. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 63 p.

Hendrickson, G.E.: Doonan, C.J. 1972. Hydrology and recreation on the cold-water rivers of Michigan's southern peninsula. Water Inf. Sere Rep. 3. Okemos, MI: U.S. Department of the Interior, Geological Survey. 83 p.

Hendrickson, G.E.; Knutilla, R.L.; Doonan, C.J. 1973a. Hydrology and recreation of selected cold-water rivers of the St. Lawrence River basin in Michigan, New York, and Wisconsin. Water-Resour. Invest. 8-73. Okemos, MI: U.S. Department of the Interior, Geological Survey. 73 p.

Hendrickson, G.E.; Knutilla, R.L.; Doonan, C.J. 1973b. Hydrology and recreation on the cold-water rivers of Michigan's upper peninsula. Water Inf. Sere Rep. 4. Okemos, MI: U.S. Department of the Interior, Geological Survey. 39 p.

Hughes, Robert M.; Omernik, James M. 1981. A proposed approach to determine regional patterns in aquatic ecosystems. In: Armantrout, N.B., ed. Acquisition and utilization of aquatic habitat inventory information. Bethesda, MD: Western Division, American Fisheries Society: 92-102.

Hughes, Robert M.; Rexstad, Eric; Bond, Carl E. 1987. The relationship of aquatic ecoregions, river basins and physiographic provinces to the ichthyogeographic regions of Oregon. Copeia. 1987: 423-432.

Hunt, Robert L. 1971. Responses of a brook trout population to habitat development in Lawrence Creek. Tech. Bull. 48. Madison, WI: Wisconsin Department of Natural Resources. 35 p.

Hunt, Robert L. 1979. Removal of woody streambank vegetation to improve trout habitat. Tech. Bull. 115. Madison, WI: Wisconsin Department of Natural Resources. 36 p.

Johnson, Douglas H. 1981. The use and misuse of statistics in wildlife habitat studies. In: Capen, D.E., ed. The use of multivariate statistics in studies of wildlfie habitat. Gen. Tech. Rep. RM-87. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 11-19.

Klamt, Robert R. 1976. The effects of coarse granitic sediment on the distribution and abundance of salmonids in the central Idaho batholith. Moscow, ID: University of Idaho. 85 p. M.S. thesis.

Konopacky, Richard Charles. 1984. Sedimentation and productivity in salmonid streams. Moscow, ID: University of Idaho. 197 p. Ph.D. dissertation.

Kraft, Melvin E. 1972. Effects of controlled flow reduction on a trout stream. Journal of the Fisheries Research Board of Canada. 29: 1405-1411.

Lanka, Robert P. 1985. Modeling trout standing stock in small Wyoming streams based upon easily measured habitat and geomorphological characteristics. Laramie, WY: University of Wyoming. 102 p. M.S. thesis.

Lanka, Robert P.; Hubert, Wayne A.; Wesche, Thomas A. 1987. Relations of geomorphology to stream habitat and trout standing stock in small Rocky Mountain streams. Transactions of the American Fisheries Society. 116: 21-28.

Larsen, D.P.; Omernik, J.M.; Hughes, R.M. [and others]. 1986. Correspondence between spatial patterns in fish assemblages in Ohio streams and aquatic ecoregions. Environmental Management. 10: 815-828.

Latta, W.C. 1965. Relationship of the young-of-the-year trout to mature trout and groundwater. Transactions of the American Fisheries Society. 94: 32-39.

Layher, William George. 1983. Habitat suitability for selected adult fishes in prairie streams. Stillwater, OK: Oklahoma State University. 333 p. Ph.D. dissertation.

Leathe, Stephen A.; Bartelt, Steve; Morris, Lani M. 1985. Cumulative effects of micro-hydro development on the fisheries of the Swan River drainage, Montana. Vol. 2: Technical information. Portland, OR: U.S. Department of Energy, Bonneville Power Administration; final report, project 82-19. 106 p.

Leathe, Stephen A.; Enk, Michael D. 1985. Cumulative effects of micro-hydro development on the fisheries of the Swan River drainage, Montana. Vol. 1: Summary report. Portland, OR: U.S. Department of Energy, Bonneville Power Administration; final report; project 82-19. 114 p. and appendices.

Leathe, Stephen A.; Graham, Patrick J. 1983. Cumulative effects of micro-hydro development on the fisheries of the Swan River drainage, Montana. Portland, OR: U.S. Department of Energy, Bonneville Power Administration; first annual report, project 82-19. 65 p. and appendix.

Levins, Richard. 1966. The strategy of model building in population biology. American Scientist. 54: 421-431.

Lewis, S.L. 1969. Physical factors influencing fish populations in pools of a trout stream. Transactions of the American Fisheries Society. 98: 14-19.

Li, Hiram W.; Schreck, Carl B.; Rodnick, Kenneth J. 1984. Assessment of habitat quality models for cutthroat trout *(Salmo clarki clarkI)* and coho salmon *(Oncorhynchus kisutch)* for Oregon's coastal streams. In: Terrell, J.W., ed. Proceedings of a workshop on fish habitat suitability index models; 1983 February 14-15; Fort Collins, CO. Biol. Rep. 85(6). Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service: 57-111.

Loar, J.M. [and others] eds. 1985. Application of habitat evaluation models in southern Appalachian trout streams. Publ. 2383. Oak Ridge, TN: U.S. Department of Energy. Environmental Sciences Division, Oak Ridge National Laboratory. 310 p.

Lotspeich, Frederick B. 1980. Watersheds as the basic ecosystem: this conceptual framework provides a basis for a natural classification system. Water Resources Bulletin. 16: 581-586.

Lotspeich, Frederick B.; Platts, William S. 1982. An integrated land-aquatic classification system.; North American Journal of Fisheries Management. 2: 138-149.

Marshall, Steven A. 1985. Survival, movement, and habitat utilization of spring-stocked fingerling brown trout *(Salmo trutta)* in six northeast Iowa streams. Ames, IA: Iowa State University. 42 p. M.S. thesis.

McClendon, Danny D.; Rabeni, Charles F. 1985. Habitat models for centrarchids of the Ozark national scenic riverways. Columbia, MO: Missouri Cooperative Fish and Wildlife Research Unit, University of Missouri; completion report to the National Park Service; contract PX 6000-3-0393. 131 p.

McFadden, J.T.; Cooper, E.L. 1962. An ecological comparison of six populations of brown trout *(Salmo trutta).* Transactions of the American Fisheries Society. 91 : 53-62.

McKernan, Donald L.; Johnson, Donald R.; Hodges, John I. 1950. Some factors influencing the trends of salmon populations in Oregon. Transactions of the North American Wildlife Conference. 15: 427-449.

Mullan, James W. 1983. Should we agree that some standardized minimum set of stream habitat components should be measured by everyone, regardless of the habitat evaluation methods utilized? Proceedings of the Western Game and Fish Commissioners Annual Meeting. 63: 202-211.

Murphy, M.L.; Hawkins, C.P.; Anderson, N.H. 1981. Effects of canopy modification and accumulated sediment on stream communities. Transactions of the American Fisheries Society. 110: 469-478.

Nehring, A. Barry. 1979. Evaluation of instream flow methods and determination of water quantity needs for streams in the State of Colorado. Fort Collins, CO: Colorado Division of Wildlife; final report to U.S. Fish and Wildlife Service, Cooperative Instream Flow Service Group, contract 14-16-0006-78-909. 144 p.

Nehring, A.B.; Anderson, A.M. 1981. Stream fisheries investigations. Fort Collins, CO: Colorado Division of Wildlife; job progress report; Federal aid project F-51-R. 161 p.

Nehring, A.B.; Anderson, R.M. 1982. Stream fisheries investigations. Fort Collins, CO: Colorado Division of Wildlife; job progress report; Federal aid project F-51-R. 185 p.

Nehring, A.B.; Anderson, A.M. 1983. Stream fisheries investigations. Fort Collins, CO: Colorado Division of Wildlife; job progress report; Federal aid project F-51-R. 188 p.

Nehring, R.B.; Anderson, A.M. 1984. Stream fisheries investigations. Fort Collins, CO: Colorado Division of Wildlife; job progress report, Federal aid project F-51-R. 203 p.

Nelson, Frederick A. 1980. Evaluation of four instream flow methods applied to four trout rivers in southwest Montana. Bozeman, MT: Montana Department of Fish, Wildlife, and Parks; final report to U.S. Fish and Wildlife Service; contract 14-16-0006- 78-046. 1 01 p. .

Neter, J.; Wasserman., W. 1974. Applied linear statistical models. Homewood,IL: R.D. Irwin, Inc. 842 p.

Nickelson, Thomas. 1976. Development of methodologies for evaluating instream flow needs for salmonid rearing. In: Orsborn, J.F.; Auman, C.H., eds. Instreamflow needs. Bethesda, MD: American Fisheries Society: 588-596. Vol. 2.

Nickelson, Thomas E.; Beidler, Willard M.; Willis, Mitchell J. 1979. Streamflow requirements of salmonids. Portland, OR: Oregon Department of Fish and Wildlife; final report; Federal aid project AFS-62. 30 p.

Omernlk, J.M.; Gallant, A.L. 1986. Ecoregions of the Pacific Northwest. EPA/600/3-86/033. Corvallis, OR: U.S. Environmental Protection Agency. 39 p. and map.

Omernlk, J.M.; Shirazi, M.A.; Hughes, R.M. 1981. A synoptic approach for regionalizing aquatic ecosystems. In: Inplace resource inventories: principles and practices, a national workshop; 1981 August 9-14; Orono, Maine: University of Maine. [Location of publisher unknown]: Society of American Foresters: 199-218.

Orth, Donald J.; Jones, Ray N.; Maughan, O. Eugene. 1981. Considerations in the development of curves for habitat suitability criteria. In: Armantrout, N.B., ed. Acquisition and utilization of aquatic habitat inventory information. Bethesda, MD: Western Division, American Fisheries Society: 124-133.

Orth, Donald J.; Maughan, O. Eugene. 1982. Evaluation of the incremental methodology for recommending instream flows for fishes. Transactions of the American Fisheries Society. 111: 413-445.

Oswood, M.E.; Barber, W.E. 1982. Assessment of fish habitat in streams: goals, constraints, and a new technique. Fisheries. Bethesda, MD: American Fisheries Society; 7(4): 8-11.

Otis, David L.; Burnham, Kenneth P.; White, Gary C.; Anderson, David R. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs. 62. 135 p.

Paragamian, Vaughn L. 1981. Some habitat characteristics that affect abundance and winter survival of smallmouth bass in the Maquoketa River, Iowa. In: Krumholz, L.A., ed. Proceedings of the warmwater streams symposium; 1980 March 9-11; Knoxville, TN. Bethesda, MD: American Fisheries Society: 45-53.

Parsons, Milton G.; Maxwell, James R.; Heller, David. 1981. A predictive fish habitat index model using geomorphic parameters. In: Armantrout, N.B., ed. AcquisiUon and utilization of aquatic habitat inventory information. Bethesda, MD: Western Division, American Fisheries Society: 85-91.

Pfankuch, D.J. 1975. Stream reach inventory and channel stability index. Boise, ID: U.S. Department of Agriculture, Forest Service, Northern Region. 26 p.

Platt, S.R. 1968. Strong inference. Science. 146: 347-353.

Platts, W.S. 1974. Geomorphic and aquatic conditions influencing salmonids and stream classification. [Publisher's location unknown]: U.S. Department of Agriculture, Forest Service, Surface Environment and Mining Program. 199 p.

Platts, W.S. 1976. Validity of methodologies to document stream environments for evaluating fishery conditions. In: Orsborn, J.F.; Allman, C.H., eds. Instream flow needs. Bethesda, MD: American Fisheries Society: 267-284. Vol. 2.

Platts, William S. 1981. Stream inventory garbage in--reliable analysis out: only in fairy tales. In: Armantrout, N.B., ed. Acquisition and utilization of aquatic habitat inventory information. Bethesda, MD: Western Division, American Fisheries' Society: 75-84.

Platts, William S. 1983. How many stream habitat evaluation systems do we need?--less than a million. Proceedings of the Western Game and Fish Commissioners Annual Meeting. 63: 212-220.

Platts, William S.; Megahan, Walter F.; Minshall, G. Wayne. 1983. Methods for evaluating stream, riparian, and biotic conditions. Gen. Tech. Rep. INT-138. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 70 p.

Rabern, Donald Anthony. 1984. Development of habitat based models for predicting standing crops of nine species of riverine fishes in Georgia. Athens, GA: University of Georgia. 127 p. M.S. thesis.

Randolph, Christopher L.; White, Robert G. 1984. Validity of the wetted perimeter method for recommending instream flows for salmonids in small streams. Bozeman, MT: Montana Water Resources Research Center, Montana State University; research project technical completion report. 103 p.

Rinne, J.N. 1978. Development of methods of population estimation and habitat evaluation for management of the Arizona and Gila trouts. In: Moring, J.R., ed. Proceedings of the wild trout-catchable trout symposium; 1978 February 15-17; Eugene, OR. Portland, OR: Oregon Department of Fish and Wildlife.

Rinne, John, N. 1981. Problems associated with habitat evaluation of an endangered fish in headwater environments. In: Armantrout, N.B., ed. Acquisition and utilization of aquatic habitat inventory information. Bethesda, MD: Western Division, American Fisheries Society: 202-209.

Scarnecchia, Dennis L. 1981. Effects of streamflow and upwelling on yield of wild coho salmon *(Oncorhynchus kisutch)* in Oregon. Canadian Journal of Fisheries and Aquatic Sciences. 38: 471-475.

Scarnecchia, Dennis L. 1983. Trout and char production in Colorado's small streams. Fort Collins, CO: Colorado State University. 190 p. Ph.D. dissertation.

Sekulich, Paul Thomas. 1980. The carrying capacity of infertile forest streams for rearing juvenile chinook salmon. Moscow, ID: University of Idaho. 156 p. Ph.D. dissertation.

Snedecor, George W.; Cochran, William G. 1967. Statistical methods. 6th ed. Ames, IA: Iowa State University Press. 593 p.

Sokal, Robert R.; Rohlf, F. James. 1981. Biometry. 2d ed. San Francisco: W.H. Freeman and Company. 859 p.

Solomon, David J.; Paterson, Donald. 1980. Influence of natural and regulated streamflow on survival of brown trout *(Salmo trutta* L.) in a chalkstream Environmental Biology of Fishes. 5: 379-382.

Stalnaker,C.B. 1979. The use of habitat structure preferenda for establishing flow regimes necessary for maintenance of fish habitat. In: Ward, J.V.; Stanford, J.A., eds. The ecology of regulated streams. New York: Plenum Press: 321-337.

Stevens, D.E. 1977. Striped bass *(Marone saxatilis)* year class strength in relation to river flow in the Sacramento-San Joaquin estuary, California. Transactions of the American Fisheries Society. 106: 34-42.

Stevens, D.E.; Miller, L.W. 1983. Effects of river flow on abundance of young chinook salmon, American shad, longfin smelt, and delta smelt in the Sacramento-San Joaquin River system. North American Journal of Fisheries Management. 3: 425-437.

Stewart, Phillip A. 1970. Physical factors influencing trout density in a small stream. Fort Collins, CO: Colorado State University. 78 p. M.S. thesis.

Stowell, Rick; Espinosa, Al; Bjornn, Ted, C. [and others]. 1983. Guide for predicting salmonid response to sediment yields in Idaho batholith watersheds. Ogden, UT: U.S. Department of Agriculture, Forest Service, Northern and Intermountain Regions. 95 p.

Stuber, R.J. 1985. Use of a habitat model to evaluate stream habitat improvement. In: Proceedings of the Colorado-Wyoming Chapter of the American Fisheries Society; 1985 March 20-21; Laramie, WY. Denver, CO: Colorado-Wyoming Chapter of the American Fisheries Society; 20: 76-87.

Swanston, Douglas N.; Meehan, William R.; McNutt, James A. 1977. A quantitative geomorphic approach to predicting productivity of pink and chum salmon streams in southeast Alaska. Res. Pap. PNW-227. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 16 p.

Terrell, J. W., ed. 1984. Proceedings of a workshop on fish habitat suitability index models. 1983 February 14-15; Biol. Rep. 85(6). Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service. 393 p.

Terrell, J.W.; Nickum, J.G. 1984. Workshop synthesis and recommendations. Terrell, J.W., ed. In: Proceedings of a workshop on fish habitat suitability index models. Fort Collins, Co: Biol. Rep. 85(6). Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service: 1-16.

U.S. Fish and Wildlife Service. 1980. Ecological services manual-habitat evaluation procedures (HEP). ESM 102. Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service. [Chapters are paginated individually].

U.S. Fish and Wildlife Service. 1981. Ecological services manual-standards for the development of habitat suitability index models. ESM 103. Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service. [Chapters are pagi nated individually]. .

Vernon, E.H.1958. . An examination of factors affecting the abundance of pink salmon in the Fraser River. New Westminster,)3C: International Pacific Salmon. Fisheries Commission; progress report 5. 49 p.

Ward, B.R.; Slaney, P.A. 1980. Evaluation of in-stream enhancement structures for the production of juvenile steelhead trout and coho salmon in the Keogh River: progress in 1977 and 1978. In: Proceedings of the trout stream habitat improvement workshop; 1980 November 3-6; Asheville, NC. [Publisher's location unknown): U.S. Department of Agriculture, Forest Service; Trout Unlimited: 8-15.

Weisberg, Sanford. 1980. Applied linear regression. New York: John Wiley and Sons. 283 p.

Wesche, T.A. 1974. Relationship of discharge reductions to available trout habitat for recommending suitable streamflow. Water Resour. Sere 53. Laramie, WY: Water Resources Research Institute. 73 p.

Wesche, Thomas A. 1976. Development and application of a trout cover rating system for IFN determinations. In: Orsborn, J.F.; Allman, C.H., eds. Instream flow needs. Bethesda, MD: American Fisheries Society: 224-234. Vol. 2.

Wesche, T.A. 1980. The WRRI trout cover rating method: development and . application. Water Resour. Sere 78. Laramie, WY: Water Resources Research Institute. 46 p.

Wesche, Thomas A. 1983. Overview of instream habitat evaluation methods currently applied in the western region. Proceedings of the Western Game and Fish Commissioners Annual Meeting. 63: 191-201.

Wesche, Thomas A.; Reiser, Dudley W.; Wichers, William F.; Wichers, Donna L. 1977. Fishery resources and instream flow recommendations for streams to be impacted by Cheyenne's proposed phase II development. Laramie, WY: Water Resources Research Institute, University of Wyoming; report submitted to Wyoming Game and Fish Department. 6 p. and appendix.

White, Gary C.; Anderson, David R.; Burnham, Kenneth P.; Otis, David L. 1982. Capture-recapture and removal methods for sampling closed populations. LA-8787-NERP. Los Alamos, NM: Los Alamos National Laboratory. 235 p.

White, Ray J. 1975. Trout population responses to streamflow fluctuation and habitat management in Big Roche-a-Cri Creek, Wisconsin. Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie. 19: 2469-2477.

White, Ray J. 1983. Why evaluate habitat? Proceedings of the Western Game and Fish Commissioners Annual Meeting. 63: 175-179.

White, Ray J.; Hansen, Edward A.; Alexander, Gaylord R. 1976. Relationship of trout abundance to stream flow in midwestern streams. In: Orsborn, J.F.; Allman, C.H., eds. Instream flow needs. Bethesda, MD: American Fisheries Society: 597-615. Vol. 2.

White, Ray J.; Wells, Jerry D.; Peterson, Mary E. 1983. Effects of urbanization on physical habitat for trout in streams. Bozeman, MT: Montana Water Resources Research Center, Montana State University; research project technical completion report A-134-MONT. 41 p.

Wickett, W.P. 1958. Review of certain environmental factors affecting the production of pink and chum salmon. Journal of the Fisheries Research Board of Canada. 15: 1103-1126.

Ziemer, G.L. 1973. Quantitative geomorphology of drainage basins related to fish production. Info Leaf!. 162. Juneau, AK: Alaska Department of Fish and Game. 26 p.

Appendix

Tables 1-5 show characteristics of the 99 models predicting standing crop of stream fish from habitat variables. The models are divided into five categories by the types of habitat variables found significantly related to standing crop: primarily drainage basin variables (table 1), primarily variables of channel morphometry and flow (table 2), primarily habitat-structure, biological, physical, and chemical variables (table 3), a combination of several types of variables (table 4), and tests of weighted usable area as a habitat model (table 5). Throughout all the tables the three types of independent habitat variables are denoted by letters: **A** = drainage basin variables, **B** = channel-morphometry and flow variables and **C** = habitat-structure, biological, physical, and chemical variables. In tables 1-5, models are divided into two groups by sample size ($N \geq 20$ and $N < 20$), and are then ordered by the coefficient of determination (r^2 or R^2). The statistical significance (P) of each model is shown except where it was not ›ported (nr) .The code "na" indicates that information was either not available or not appropriate. Model types were simple linear regression (LR), .multiple linear regression (MLR), correlation (C), power (P) and exponential (E) functions, and polynomial ıctions (PL). For correlations, the square of the reported correlation coefficient is shown to compare with r^2 or R^2. Some models Incorporated one or more Indices (I) that were combinations of other independent variables. Others included the logarithm g), square (X^2), or cube (X^3) of an independent variable. Where power or ɔonential, functions were fitted, the logarithmic transformations of dependent and independent variables used in the analysis are given (see equations 2 and 3 in text). Binns (1979) and Layher (1983) use ratings of variables instead of raw measurements (see text for full explanation). The individual habitat variables found significant in each model are listed by the three variable types (shown as the bold letters **A**, **B**, and **C**) using abbreviated acronyms that are defined in table 9. The number of each of the three types of habitat variables measured by investigators and used in building models is shown. The number of models is given when several statistically significant ones were developed ($p \leq 0.05$; a few investigators used larger significance values), but only characteristics of the best model accounting for the most, variation in standing crop are shown. When additional data were collected to test the model, the sample size is listed. Table 6 lists scientific names of fishes presented in the text. Tables 7 and 8 are lists of the models ordered by number and author, respectively. Table 10 lists habitat variables found to be significantly related to standing crop of stream fish in three or more models.

Table 1—Characteristics of models predicting standing crop primarily from drainage basin variables

Model number	Author	N for model	Degrees of freedom	Number of independent variables in model	r^2 or R^2 for model	P for model	Model type	Model output	Output units	Significant independent variables	Number of different variables assessed	Number of models developed	N for model test
							MODELS WITH N≥20						
1.05	Lanka (1985)	26	21	4	0.64	<0.001	MLR	Trout in rangeland streams	kg/ha	A:BP,logG,RMBE B:RWDR	11A,10B	3	8
1.04	Lanka (1985)	65	60	4	.51	<.001	MLR	Trout in forest streams	kg/ha	A:DD,RE,logRR B:logMW	11A,10B	3	11
1.01	Ziemer (1973)	21	19	1	.34[a]	nr	P,I[b]	Pink salmon	log escapement	A:DD,MBL,MBS	4A	2	
							MODELS WITH N<20						
1.03	Wesche and others (1977)	12	10	1	.66	nr	LR,I	Cutthroat trout >6 in	no./mi	A:DA,MBE,MBL,MBS, TSL	7A	1	
1.02	Burton and Wesche (1974)	11	9	1	.33	nr	P,I[b]	Trout	log no./acre	A:DA,FA,MBE,TSL	13A,5B	1	

[a] Our calculation of the coefficient of determination of log transformed power function after 3 outliers justified by Ziemer (1973) were removed.
[b] Several variables were combined into an index. The logarithm of the index was then used to determine the power function by linear regression (see equation 3 in text).

Table 2—Characteristics of models predicting standing crop primarily from channel morphometry and flow variables

Model number	Author	N for model	Degrees of freedom	Number of independent variables in model	r^2 or R^2 for model	P for model	Model type	Model output	Output units	Significant independent variables	Number of different variables assessed	Number of models or correlations developed
						MODELS WITH N≥20						
2.15	Randolph and White (1984)	40	38	1	0.98	nr	C	Rainbow trout	no. remaining/section	**B:**F11P	10B,6C	44
2.04	Kraft (1972)	20	13	6	.83	.01	MLR	Age I and older brook trout	no./pool	**B:**F,MPD,MPV, PA,XPV **C:**AC	5B,1C	4
2.16	Chisholm and Hubert (1986)	24	19	4	.69	.0001	MLR	Brook trout	kg/km	**B:**MD,MW,SG, WDR	5B	1
						MODELS WITH N<20						
2.09	Nelson (1980)	4	2	1	.996	<.05	LR	Age II+ and older trout	no./1000 ft	**B:**NSF	2B,1C	10
2.08	Hunt (1979)	8	6	1	.99	<.01	C	Brook trout	lb/mi	**B:**MSF	1B	3
2.13	Nehring and Anderson (1981, 1982, 1983, 1984)	4	2	1	.98	nr	C,P[a]	Age I+ rainbow trout	log no./ha	**B:**XSF1P	1B	4
2.12	Nehring and Anderson (1981, 1982, 1983, 1984)	4	2	1	.98	nr	C,P[a]	Age 0+ brown trout	log no./ha	**B:**XSF	4B	10
2.14	Frenette and others (1984)	7	3	3	.96	nr	MLR	Atlantic salmon parr	no./ha	**B:**MSF2P,NSPF1P, NSPF2P	4B	10
2.06	White and others (1976)	9	5	3	.95	<.001	MLR	Age 0 trout	no./km	**B:**MSF,MWF, XSPF	6B,1C	7
2.07	White and others (1976)	8	5	2	.94	.001	MLR	Trout	kg/km	**B:**MSF **C:**PSC	4B,2C	8
2.11	Nehring and Anderson (1981, 1982, 1983, 1984)	5	3	1	.88	nr	C	Age II+ brown trout	no./ha	**B:**DWF3P	1B	5
2.03	Hunt (1971)	17	10	6	.85	<.01	MLR	Brook trout	lb/100 yd	**B:**MD,MPD,PA, SA,V **C:**LUB	5B,1C	8
2.01	Burns (1971)	7	5	1	.81	<.05	C	Salmonids	kg	**B:**SA	4B	4
2.02	Burns (1971)	7	5	1	.80	<.05	C	Teleosts	kg	**B:**SA	4B	2
2.05	White (1975)	8	6	1	.76	<.01	C	Trout	kg/100 m	**B:**MWF	1B	1
2.10	Solomon and Paterson (1980)	5-7	na	1	.nr[b]	<.02	E	Age 0 brown trout	log no.	**B:**MSPF	1B	3

[a] Correlation analysis was done using linear, exponential, and power function models.
[b] The best model could not be determined because the coefficients of determination were not reported by the investigators.

Table 3—Characteristics of models predicting standing crop primarily from habitat-structure, biological, physical, and chemical variables

Model number	Author	N for model	Degrees of freedom	Number of independent variables in model	r^2 or R^2 for model	P for model	Model type	Model output	Output units	Significant independent variables	Number of different independent variables assessed	Number of models or correlations developed	N for model test
						MODELS WITH N ≥20							
3.08	Barber and others (1981a)	76	72	3	0.76	nr	MLR	Age 0 coho salmon	log no./30 m	C:AOV,DAY,log SSA	2B,15C	2	
3.04	Harshbarger and Bhattacharyya (1981)	100	93	6	.66	nr	MLR	Age II trout	biomass	C:AC,AOV<1,AOV 1-2,NR,PB,PIBV	18C	24	
3.12	Barber and others (1981a)	76	71	4	.60	nr	MLR	Coastrange sculpin	log no./30 m	C:DAY,logDS,log SS,logSSA	2B,15C	2	
3.24	McClendon and Rabeni (1985)	20	16	3	.59	nr	MLR	Rock bass ≥135 mm	no./ha	C:AAV,AB,ACS	1A,8B,22C	4	
3.11	Barber and others (1981a)	76	73	2	.56	nr	MLR	Coastal cutthroat trout	log no./30 m	B:CW C:BS	6B,9C	2	
3.10	Barber and others (1981a)	76	73	2	.54	nr	MLR	Dolly Varden	log no./30 m	B:logPW,logRW	6B,9C	2	
3.09	Barber and others (1981a)	76	71	4	.49	nr	MLR	Age I and older coho salmon	log no./30 m	B:SG C:AOV,AUB, logSS	2B,15C	2	
						MODELS WITH N <20							
3.21	Stowell and others (1983)	7	5	1	.99	<0.005	E	Age 0 chinook salmon[a]	log no./m^2	C:PE	1C	1	
3.19	Stowell and others (1983)	5	2	2	.99	<.005	PL	Age I steelhead[b]	no./m^2	C:PE^2,PE^3	1C	1	
3.15	Gordon and MacCrimmon (1982)	4	2	1	.98	<.01	C	Juvenile salmonids	no./m^2	C:PIC	1A,3B,4C	5	
3.07	Wesche (1980)	4	2	1	.95	<.05	LR,I	Brown trout[c]	lb/acre	B:ADW C:ARBV,LUB, PRBV,PUB	1B,4C	4	
3.03	Enk (1977)	8	6	1	.93	<.01	LR	Brook trout ≥100 mm	kg/100 m	C:LUB	1C	24	
3.20	Stowell and others (1983)	8	5	2	.92	.01	PL	Age 0 chinook salmon[b]	no./m^2	C:PE,PE^2	1C	1	
3.13	Paragamian (1981)	11	9	1	.90	<.001	E	Smallmouth bass ≥200 mm	log kg/ha	C:PS16-256	4B,1C	8	
3.22	Stowell and others (1983)	8	6	1	.90	.01	E	Age 0 steelhead[a]	log no./m^2	C:PE	1C	1	
3.18	Stowell and others (1983)	12	9	2	.87	.001	PL	Age 0 steelhead[b]	no./m^2	C:PE,PE^2	1C	1	
3.17	Hawkins and others (1983)	6	4	1	.85	<.01	C	Cottids	g/m^2	C:ID	2C	3	
3.16	Hawkins and others (1983)	8	6	1	.72	<.01	C	Salmonids	no./m^2	C:PS<1	2C	5	
3.01	McFadden and Cooper (1962)	5	3	1	.72	<.25	C	Nonsalmonids[d]	lb/acre	C:C	1C	0[e]	
3.14	Eifert and Wesche (1982)	17	15	1	.71	<.10	LR	Trout	kg/km	C:ARBV	19B,41C	27	
3.05	Ward and Slaney (1980)	15	13	1	.69	<.001	C	Steelhead parr	no.	C:NR>30	1C	2	
3.23	McClendon and Rabeni (1985)	10	7	2	.62	<.05	MLR	Smallmouth bass ≥150 mm	no./ha	C:AB,AUB	1A,8B,22C	4	10
3.06	Wesche (1980)	8	6	1	.60	<.05	LR,I	Brown trout[f]	lb/acre	C:ARBV,LUB,PRBV, PUB	4C	4	
3.25	McClendon and Rabeni (1985)	10	7	2	.59	<.05	MLR	Longear sunfish ≥100 mm	no./ha	C:ACS,AWW	1A,8B,22C	4	10
3.02	Klamt (1976)	15	12	2	.36	nr	C	Salmonids	no./m^2	C:ID,PBL	4B,5C	5	

[a] Models were developed for fish in pools in winter.
[b] Models were developed for fish in runs in summer.
[c] Model for large streams (>100 ft^3/s). Independent variables were combined in an index.
[d] Includes 14 species of Catostomidae, Cyprinidae, Ictaluridae, and Percidae.
[e] No correlations significant at P≤0.10.
[f] Model for small streams (<100 ft^3/s). Independent variables were combined in an index.

Table 4—Characteristics of models predicting standing crop from several types of independent variables

Model number	Author	N for model	Degrees of freedom	Number of independent variables in model	r^2 or R^2 for model	P for model	Model type	Model output
				MODELS WITH N≥20				
4.28	Rabern (1984)	75	63	11	.98	.0001	MLR,PL[e]	American eel
4.09	Binns (1979), Binns and Eiserman (1979)	36	30	5	.97	nr	P,MLR,I[b]	Trout
4.34	Rabern (1984)	75	66	8	.96	.0001	MLR,PL[e]	Warmouth
4.29	Rabern (1984)	75	62	12	.96	.0001	MLR	Gizzard shad
4.10	Nickelson and others (1979)	29	27	1	.91	nr	LR,I	Age 1+ and older cutthroat trout
4.13	Sekulich (1980)	80	76	3	.89	.008	MLR	Age 0 chinook salmon in pools
4.31	Rabern (1984)	75	63	11	.87	.0001	MLR	Lake chubsucker
4.39	Marshall (1985)	24	19	4	.86	nr	MLR	Age 0+ brown trout
4.27	Rabern (1984)	75	67	7	.85	.0001	MLR	Bowfin
4.33	Rabern (1984)	75	58	16	.85	.001	MLR	Brown bullhead
4.26	Konopacky (1984)	21	17	3	.82	<.01	MLR	Age 0 chinook salmon
4.36	Leathe and Enk (1985)	21	15	5	.81	<.05	MLR	Bull trout ≥75 mm
4.35	Rabern (1984)	75	68	6	.80	.0001	MLR,PL[e]	Spotted sunfish
4.11	Nickelson and others (1979)	23	21	1	.79	nr	LR,I	Juvenile steelhead
4.32	Rabern (1984)	75	66	8	.78	.0001	MLR	Spotted sucker
4.30	Rabern (1984)	75	68	6	.66	.0001	MLR	Chain pickerel
4.08	Rinne (1978)	24	17	6	.52	nr	MLR	Gila trout
4.05	Hendrickson and others (1973b)	29	24	4	.47	<.10	P,MLR[c]	Trout
4.37	Leathe and Enk (1985)	35	31	3	.46	<.05	MLR	Westslope cutthroat trout ≥75 mm
4.03	Stewart (1970)	41	37	3	.43	<.05	MLR	Rainbow trout >18 cm
4.14	Fraley and Graham (1981)	134	130	3	.41	<.05	MLR	Age I and older trout
4.02	Stewart (1970)	41	38	2	.37	<.05	MLR	Brook trout >18 cm
4.07	Platts (1974, 1976)	291	270	20	.35	nr	MLR	Rainbow trout
4.38	Leathe and Enk (1985)	33	31	1	.28	<.05	C	Brook trout ≥75 mm
				MODELS WITH N<20				
4.21	Layher (1983)	14	9	4	.99	.0001	MLR	White crappie
4.19	Layher (1983)	6	2	3	.99	.001	MLR	Channel catfish
4.17	Layher (1983)	10	4	5	.97	.0007	MLR	Orangethroat darter
4.25	White and others (1983)	16	7	8	.95	nr	P,MLR[c]	Trout ≥200 mm
4.16	Layher (1983)	13	9	3	.94	.0001	MLR	Slenderhead darter
4.12	Nickelson and others (1979)	12	10	1	.94	nr	LR	Juvenile coho salmon
4.15	Layher (1983)	12	5	6	.92	.04	MLR	Spotted bass
4.18	Layher (1983)	18	12	5	.90	.0001	MLR	Central stoneroller
4.20	Layher (1983)	14	12	1	.90	.0001	LR	Largemouth bass
4.23	Scarnecchia (1983)	11	6	4	.84	nr	MLR	Trout
4.24	Scarnecchia (1983)	11	6	4	.76	nr	MLR	Trout
4.06	Hendrickson and others (1973a)	17	13	3	.74	<.10	P,MLR[c]	Trout
4.01	Lewis (1969)	19	16	2	.66	<.01	MLR	Trout ≥7 in
4.22	Layher (1983)	14	11	2	.50	.02	MLR	Green sunfish
4.04	Hendrickson and Doonan (1972)	16	14	1	.40	<.01	C,E	Trout

[a] Squared independent variables and cross-products of 2 variables were used to develop polynomial equations by multiple linear regression.
[b] Habitat variables were first converted to ratings, and some of these ratings were combined into indices. Then all ratings and indices were transformed by using logarithms and a power function of the form: $Y = aR_1^q \cdot cR_2^q \cdot \ldots \cdot yR_n^z$ (where R_i = rating or index) was calculated using multiple linear regression (see equation 3 in text).
[c] Variables were transformed to logarithms and then a power function of the form: $Y = aX_1^q \cdot cX_2^q \cdot \ldots \cdot yX_n^z$, was calculated by multiple linear regression.
[d] Independent variables were not specified by the authors.
[e] The number of independent variables of this type included in model.

Output units	Significant independent variables	Number of different independent variables assessed	Number of models or correlations developed	N for model test
		MODELS WITH N ≥20		
kg/ha	**A**:DAO,G **C**:DOR,MAL,MTOC,MTP	3A,3B,15C	5	2
log kg/ha	**B**:logRAFV,logRLSF,logRSW,logRV **C**:logRCO,logREB,logRNN,logRS,logRXST	4B,7C	2	8
kg/ha	**C**:MAL,MC,NFS	3A,3B,15C	5	2
kg/ha	**B**:MD,MMF,MW **C**:DOR,MAT,MBOD5,MC,MPCC,MTOC,MTP,NDO,R	3A,3B,15C	4	2
g/section	**B**:FD1,FD2,RV,SA **C**:FC>5,FOC>5,FT>5,FVR>5	4B,4C	2	20
g/m^2	**B**:F **C**:ED,NT5P	10B,5C	14	
kg/ha	**B**:MMF **C**:DOR,FFD,MAL,MBOD5,MC,MTH,MTP,MTU,NDO,R	3A,3B,15C	5	
kg/ha	**B**:MD,SA **C**:AOV,DS	4B,15C	2	
kg/ha	**B**:MD,MMF **C**:DOR,MAWT,MBOD5,MPCC,NFS	3A,3B,15C	5	2
kg/ha	**B**:MD,MMF,MW **C**:DOR,FFD,MAT,MAWT,MC,MPCC,MTH,MTOC,MTP,MTU, NDO,NFS,R	3A,3B,15C	3	
g/pool	**B**:logPA,RA **C**:MRPS	2B,4C	5	
$no./100\ m^2$	**A**:DA **B**:XPD **C**:AC,CD,SSC	3A,6B,9C	1	
kg/ha	**C**:DOR,NDO,NFS,R	3A,3B,15C	5	2
g/section	**B**:SA **C**:FC>5,FOC>5,FT>5,FVR>5,DVP	1B,5C	1	12
kg/ha	**A**:AR **B**:MD,MMF **C**:MAL,MAWT,MTU,NFS,R	3A,3B,15C	3	2
kg/ha	**B**:MD **C**:DOR,FFD,MAT,MAWT,NFS	3A,3B,15C	5	2
g/100 m	**B**:MPD,PA,PV,XPD **C**:AC,PAC	7B,3C	8	
log lb/acre	**B**:logMFA,logVI **C**:logMAXT,logPAV	2A,17B,17C	3	
$no./100\ m^2$	**A**:DA **B**:XD **C**:AC	3A,6B,9C	1	
g/m	**B**:MD **C**:RC1,RC2	5B,10C	7	
$no./100\ m^2$	**A**:SO **C**:AC,D90	30[d]	3	23
g/m	**B**:MD **C**:TCR	5B,10C	7	
no./section	**A**:E,WC **B**:MD,MW,PPO,PRI,SG **C**:PBS,PF(2*),PFS,PG,PR,PRA(2*),SBC(5*)	2A,5B,13C	5	
$no./100\ m^2$	**C**:AC	3A,6B,9C	1	
		MODELS WITH N<20		
kg/ha	**C**:RNN,RPH,RPO,RT	2A,12B,16C	6	9
kg/ha	**A**:RG **B**:RPP **C**:RPH	2A,12B,16C	6	23
kg/ha	**B**:RPP **C**:RCH,RSU,RTA,RWT	2A,12B,16C	5	20
log no./km	**B**:logAFV,logCPR:MF,logMV **C**:logNN,logPEB,logPTC,logRS,logXST	6B,6C	24	
kg/ha	**B**:RXW,RPR **C**:RCH	2A,12B,16C	3	11
g/section	**B**:PV	1B	1	318
kg/ha	**B**:RMD,RMW,RNW **C**:RNN,RPH,RT	2A,12B,16C	4	14
kg/ha	**B**:RMW,RPRU **C**:RMH,RPH,RSU	2A,12B,16C	6	6
kg/ha	**C**:RPH	2A,12B,16C	5	31
$g \cdot m^{-2} \cdot yr^{-1}$	**A**:E **B**:MW,WDR **C**:SU	1A,4B,10C	13	
g/m^2	**A**:E **C**:NN,P0V,SU	1A,4B,10C	14	
log lb/acre	**B**:logMFA,logWDR **C**:logPAV	2A,17B,17C	18	
no./pool	**B**:MPV **C**:AC	4B,2C	4	
kg/ha	**C**:RPH,RPO	2A,12B,16C	6	47
log lb/acre	**C**:MAXT	3B,1C	2	

Table 5—Tests of weighted usable area (WUA) as a predictor of standing crop of stream fish

Model number	Author	N for model	Degrees of freedom	Number of independent variables in model	r^2 for model	P for model	Model type	Model output	Output units	Number of models developed
				MODELS WITH N ≥20						
5.03	Nickelson and others (1979)	23	21	1	0.52	<0.05	LR	Steelhead trout	g/section	1
5.02	Nickelson and others (1979)	29	27	1	.27	<.05	LR	Cutthroat trout	g/section	1
				MODELS WITH N <20						
5.09	Nehring and Anderson (1983, 1984)	5	3	1	.96	nr	C	Age I+ brown trout	no./ha	22
5.10	Nehring and Anderson (1983, 1984)	5	3	1	.92	nr	C	Age I+ rainbow trout	no./ha	8
5.11	Gowan (1984)	6	4	1	.90	.001	LR	Trout	no./section	3
5.06	Orth and Maughan (1982)	8	6	1	.86	<.001	C	Freckled madtom	kg/ha	2
5.05	Wesche (1980)	9	7	1	.82	<.01	LR	Brown trout	lb	1
5.04	Stalnaker (1979)	19	17	1	.81	nr	LR	Brown trout	kg/km	1
5.01	Nehring (1979)	7	5	1	.76	nr	C	Brown trout >13 cm	lb/acre	1
5.14	Loar and others (1985)	nr	na	1	.74	.0004	LR[a]	Age 0 rainbow trout in allopatry	no./km	14
5.13	Loar and others (1985)	nr	na	1	.74	<.05	C[a]	Age II+ and older brown trout	g/km	35
5.08	Orth and Maughan (1982)	9	7	1	.71	<.01	C	Orangebelly darter	kg/ha	2
5.07	Orth and Maughan (1982)	8	6	1	.71	<.01	C	Central stoneroller	kg/ha	3
5.12	Loar and others (1985)	nr	na	1	.62	<.05	C	Age I+ brown trout	no./km	6

[a] Standing crop was correlated with the minimum WUA calculated from mean monthly flows (see text).

Table 6—Common and scientific names of fish species cited in text

Common name	Scientific name
American eel	*Anguilla rostrata* (Lesueur)
Atlantic salmon	*Salmo salar* Linnaeus
Bowfin	*Amia calva* Linnaeus
Brook trout	*Salvelinus fontinalis* (Mitchill)
Brown bullhead	*Ictalurus nebulosus* (Lesueur)
Brown trout	*Salmo trutta* Linnaeus
Bull trout	*Salvelinus confluentus* (Suckley)
Central stoneroller	*Campostoma anomalum* (Rafinesque)
Chain pickerel	*Esox niger* Lesueur
Channel catfish	*Ictalurus punctatus* (Rafinesque)
Chinook salmon	*Oncorhynchus tshawytscha* (Walbaum)
Coastrange sculpin	*Cottus aleuticus* Gilbert
Coastal cutthroat trout	*Salmo clarki clarki* Richardson
Coho salmon	*Oncorhynchus kisutch* (Walbaum)
Colorado River cutthroat trout	*Salmo clarki pleuriticus* Cope
Cutthroat trout	*Salmo clarki* Richardson[a]
Dolly Varden	*Salvelinus malma* (Walbaum)
Freckled madtom	*Noturus nocturnus* Jordan and Gilbert
Gila trout	*Salmo gilae* Miller
Gizzard shad	*Dorosoma cepedianum* (Lesueur)
Green sunfish	*Lepomis cyanellus* Rafinesque
Lake chubsucker	*Erimyzon sucetta* (Lacépède)
Largemouth bass	*Micropterus salmoides* (Lacépède)
Longear sunfish	*Lepomis megalotis* (Rafinesque)
Mountain whitefish	*Prosopium williamsoni* (Girard)
Orangebelly darter	*Etheostoma radiosum* (Hubbs and Black)
Orangethroat darter	*Etheostoma spectabile* (Agassiz)
Pink salmon	*Oncorhynchus gorbuscha* (Walbaum)
Prickly sculpin	*Cottus asper* Richardson
Rainbow or steelhead trout	*Salmo gairdneri* Richardson
Reticulate sculpin	*Cottus perplexus* Gilbert and Evermann
Rock bass	*Ambloplites rupestris* (Rafinesque)
Sculpin	*Cottus* sp.
Slenderhead darter	*Percina phoxocephala* (Nelson)
Smallmouth bass	*Micropterus dolomieui* (Lacépède)
Spotted bass	*Micropterus punctulatus* (Rafinesque)
Spotted sucker	*Minytrema melanops* (Rafinesque)
Spotted sunfish	*Lepomis punctatus* (Valenciennes)
Threespine stickleback	*Gasterosteus aculeatus* Linnaeus
Warmouth	*Lepomis gulosus* (Cuvier)
Westslope cutthroat trout	*Salmo clarki lewisi* (Girard)
White crappie	*Pomoxis annularis* Rafinesque

[a] Scientific name used when subspecies not reported.

Table 7—Models in numerical order with corresponding authors

Model number	Author	Model number	Author
1.01	Ziemer (1973)	4.05	Hendrickson and others (1973b)
1.02	Burton and Wesche (1974)	4.06	Hendrickson and others (1973a)
1.03	Wesche and others (1977)	4.07	Platts (1974, 1976)
1.04	Lanka (1985)	4.08	Rinne (1978)
1.05	Lanka (1985)	4.09	Binns (1979), Binns and Eiserman (1979)
2.01	Burns (1971)	4.10	Nickelson and others (1979)
2.02	Burns (1971)	4.11	Nickelson and others (1979)
2.03	Hunt (1971)	4.12	Nickelson and others (1979)
2.04	Kraft (1972)	4.13	Sekulich (1980)
2.05	White (1975)	4.14	Fraley and Graham (1981)
2.06	White and others (1976)	4.15	Layher (1983)
2.07	White and others (1976)	4.16	Layher (1983)
2.08	Hunt (1979)	4.17	Layher (1983)
2.09	Nelson (1980)	4.18	Layher (1983)
2.10	Solomon and Paterson (1980)	4.19	Layher (1983)
2.11	Nehring and Anderson (1981, 1982, 1983, 1984)	4.20	Layher (1983)
2.12	Nehring and Anderson (1981, 1982, 1983, 1984)	4.21	Layher (1983)
2.13	Nehring and Anderson (1981, 1982, 1983, 1984)	4.22	Layher (1983)
2.14	Frenette and others (1984)	4.23	Scarnecchia (1983)
2.15	Randolph and White (1984)	4.24	Scarnecchia (1983)
2.16	Chisholm and Hubert (1986)	4.25	White and others (1983)
3.01	McFadden and Cooper (1962)	4.26	Konopacky (1984)
3.02	Klamt (1976)	4.27	Rabern (1984)
3.03	Enk (1977)	4.28	Rabern (1984)
3.04	Harshbarger and Bhattacharyya (1981)	4.29	Rabern (1984)
3.05	Ward and Slaney (1980)	4.30	Rabern (1984)
3.06	Wesche (1980)	4.31	Rabern (1984)
3.07	Wesche (1980)	4.32	Rabern (1984)
3.08	Barber and others (1981a)	4.33	Rabern (1984)
3.09	Barber and others (1981a)	4.34	Rabern (1984)
3.10	Barber and others (1981a)	4.35	Rabern (1984)
3.11	Barber and others (1981a)	4.36	Leathe and Enk (1985)
3.12	Barber and others (1981a)	4.37	Leathe and Enk (1985)
3.13	Paragamian (1981)	4.38	Leathe and Enk (1985)
3.14	Eifert and Wesche (1982)	4.39	Marshall (1985)
3.15	Gordon and MacCrimmon (1982)	5.01	Nehring (1979)
3.16	Hawkins and others (1983)	5.02	Nickelson and others (1979)
3.17	Hawkins and others (1983)	5.03	Nickelson and others (1979)
3.18	Stowell and others (1983)	5.04	Stalnaker (1979)
3.19	Stowell and others (1983)	5.05	Wesche (1980)
3.20	Stowell and others (1983)	5.06	Orth and Maughan (1982)
3.21	Stowell and others (1983)	5.07	Orth and Maughan (1982)
3.22	Stowell and others (1983)	5.08	Orth and Maughan (1982)
3.23	McClendon and Rabeni (1985)	5.09	Nehring and Anderson (1983, 1984)
3.24	McClendon and Rabeni (1985)	5.10	Nehring and Anderson (1983, 1984)
3.25	McClendon and Rabeni (1985)	5.11	Gowan (1984)
4.01	Lewis (1969)	5.12	Loar and others (1985)
4.02	Stewart (1970)	5.13	Loar and others (1985)
4.03	Stewart (1970)	5.14	Loar and others (1985)
4.04	Hendrickson and Doonan (1972)		

Table 8—Authors in alphabetical order with corresponding model numbers

Author	Model number	Author	Model number
Barber and others (1981a)	3.08	Nehring and Anderson (1981, 1982, 1983, 1984)	2.11
Barber and others (1981a)	3.09	Nehring and Anderson (1981, 1982, 1983, 1984)	2.12
Barber and others (1981a)	3.10	Nehring and Anderson (1981, 1982, 1983, 1984)	2.13
Barber and others (1981a)	3.11	Nehring and Anderson (1983, 1984)	5.09
Barber and others (1981a)	3.12	Nehring and Anderson (1983, 1984)	5.10
Binns (1979), Binns and Eiserman (1979)	4.09	Nelson (1980)	2.09
Burns (1971)	2.01	Nickelson and others (1979)	4.10
Burns (1971)	2.02	Nickelson and others (1979)	4.11
Burton and Wesche (1974)	1.02	Nickelson and others (1979)	4.12
Chisholm and Hubert (1986)	2.16	Nickelson and others (1979)	5.02
Eifert and Wesche (1982)	3.14	Nickelson and others (1979)	5.03
Enk (1977)	3.03	Orth and Maughan (1982)	5.06
Fraley and Graham (1981)	4.14	Orth and Maughan (1982)	5.07
Frenette and others (1984)	2.14	Orth and Maughan (1982)	5.08
Gordon and MacCrimmon (1982)	3.15	Paragamian (1981)	3.13
Gowan (1984)	5.11	Platts (1974, 1976)	4.07
Harshbarger and Bhattacharyya (1981)	3.04	Rabern (1984)	4.27
Hawkins and others (1983)	3.16	Rabern (1984)	4.28
Hawkins and others (1983)	3.17	Rabern (1984)	4.29
Hendrickson and Doonan (1972)	4.04	Rabern (1984)	4.30
Hendrickson and others (1973a)	4.06	Rabern (1984)	4.31
Hendrickson and others (1973b)	4.05	Rabern (1984)	4.32
Hunt (1971)	2.03	Rabern (1984)	4.33
Hunt (1979)	2.08	Rabern (1984)	4.34
Klamt (1976)	3.02	Rabern (1984)	4.35
Konopacky (1984)	4.26	Randolph and White (1984)	2.15
Kraft (1972)	2.04	Rinne (1978)	4.08
Lanka (1985)	1.04	Scarnecchia (1983)	4.23
Lanka (1985)	1.05	Scarnecchia (1983)	4.24
Layher (1983)	4.15	Sekulich (1980)	4.13
Layher (1983)	4.16	Solomon and Paterson (1980)	2.10
Layher (1983)	4.17	Stalnaker (1979)	5.04
Layher (1983)	4.18	Stewart (1970)	4.02
Layher (1983)	4.19	Stewart (1970)	4.03
Layher (1983)	4.20	Stowell and others (1983)	3.18
Layher (1983)	4.21	Stowell and others (1983)	3.19
Layher (1983)	4.22	Stowell and others (1983)	3.20
Leathe and Enk (1985)	4.36	Stowell and others (1983)	3.21
Leathe and Enk (1985)	4.37	Stowell and others (1983)	3.22
Leathe and Enk (1985)	4.38	Ward and Slaney (1980)	3.05
Lewis (1969)	4.01	Wesche (1980)	3.06
Loar and others (1985)	5.12	Wesche (1980)	3.07
Loar and others (1985)	5.13	Wesche (1980)	5.05
Loar and others (1985)	5.14	Wesche and others (1977)	1.03
Marshall (1985)	4.39	White (1975)	2.05
McClendon and Rabeni (1985)	3.23	White and others (1976)	2.06
McClendon and Rabeni (1985)	3.24	White and others (1976)	2.07
McClendon and Rabeni (1985)	3.25	White and others (1983)	4.25
McFadden and Cooper (1962)	3.01	Ziemer (1973)	1.01
Nehring (1979)	5.01		

Table 9—Independent variables found significant in the best models and their abbreviations

Abbreviation	Variable	Abbreviation	Variable
	DRAINAGE BASIN (A)[a]		
AR	Annual rainfall	MBL	Mean basin length
BP	Basin perimeter	MBS	Mean basin slope
DA	Drainage area	RE	Elevation rating
DAO	Distance from Atlantic Ocean	RG	Gradient rating
DD	Drainage density	RMBE	Mean basin elevation rating
E	Reach elevation	RR	Relief ratio
FA	Forested area	SO	Stream order
G	Reach gradient from map	TSL	Total stream length
MBE	Mean basin elevation	WC	Watershed condition
	CHANNEL MORPHOMETRY (B)		
ADW	Area of deep water > 1.5 ft	RNW	Minimum width rating
CW	Channel width at bankful flow	RPP	Percentage of pool rating
FD1	Frequency of depth 46-60 cm	RPR	Percentage of riffle rating
FD2	Frequency of depth >60 cm	RPRU	Percentage of run rating
MD	Mean depth	RSW	Stream width rating
MPD	Mean pool depth	RW	Riffle width
MW	Mean width	RWDR	Rating of width-to-depth ratio
PA	Pool area	RXW	Maximum width rating
PPO	Percentage of pool	SA	Surface area
PRI	Percentage of riffle	SG	Section gradient measured in field
PV	Pool volume	V	Channel volume
PW	Pool width	WDR	Width-to-depth ratio
RA	Riffle area	XD	Maximum depth
RMD	Mean depth rating	XPD	Maximum pool depth
RMW	Mean width rating		
	FLOW[b] (B)		
AFV	Annual flow variation	MSPF	Mean spring flow
CPF:MF	Critical period flow as percent of mean flow	MV	Mean velocity
		MWF	Mean winter flow
F	Flow	NSF	Minimum summer flow
F11P	Flow 11 days previous	NSPF1P	Minimum spring flow 1 year previous
DWF3P	Difference between 7-day maximum and 7-day minimum winter flows 3 years previous	NSPF2P	Minimum spring flow 2 years previous
		RAFV	Annual flow variation rating
		RLSF	Late summer flow rating
MFA	Mean flow per unit area	RV	Velocity rating
MMF	Mean monthly flow	VI	Velocity index
MPV	Mean pool velocity	XPV	Maximum pool velocity
MSF	Mean summer flow	XSF	Maximum summer flow
MSF2P	Mean summer flow 2 years previous	XSF1P	Maximum summer flow 1 year previous
		XSPF	Maximum spring flow
	HABITAT STRUCTURE (C)		
AAV	Area of aquatic vegetation	LUB	Length of undercut bank
AC	Area of all cover	NR	Number of rocks
AOV	Area of overhanging riparian vegetation	NR>30	Number of rocks >30 cm
		PAC	Percentage of area as cover
AOV<1	Area of overhanging riparian vegetation <1 m above water	PAV	Percentage of area as aquatic vegetation
		PB	Percentage of pool area as brush cover
AOV1-2	Area of overhanging riparian vegetation 1-2 m above water	PBL	Percentage of area as boulder and log cover

Footnotes are at end of table.

Table 9—Independent variables found significant in the best models and their abbreviations (continued)

Abbreviation	Variable	Abbreviation	Variable
	HABITAT STRUCTURE (C) (continued)		
ARBV	Area of rubble, boulder, and aquatic vegetation substrate	PEB	Percentage of eroding bank
		PF	Pool feature
AUB	Area of undercut bank	PIBV	Percentage of area as instream bank vegetation
AWW	Area of water willow	PIC	Percentage of area as instream cover
BS	Bank stability rating	POV	Percentage of zero velocity
CD	Channel debris	PRA	Pool rating
DS	Deep slow area	PTC	Pool and turbulence cover
FC>5	Frequency of cover in water >5 cm deep	RC1	Rock cover <0.1 m^2
FOC>5	Frequency of overhanging cover in water >5 cm deep	RC2	Rock cover >0.3 m^2
		RCO	Rating of cover
FT>5	Frequency of turbulence in water >5 cm deep	REB	Rating of eroding banks
		SBC	Streambank condition
FVR>5	Frequency of velocity refuge in water >5 cm deep	SS	Shallow slow area
		TCR	Total cover rating
	BIOLOGICAL (C)		
DAY	Days from June 1	NFS	Number of fish species
DVP	Depth and velocity preference factors	PRBV	Preference factor for rubble, boulder, and aquatic vegetation
ED	Estimate of eggs deposited per m^2	PUB	Preference factor for undercut bank
		PSC	Previous standing crop
ID	Invertebrate drift abundance	R	Species range
	PHYSICAL (C) - SUBSTRATE		
AB	Area of boulder substrate	PG	Percentage of gravel substrate
ACS	Area of cobble substrate	PR	Percentage of rubble substrate
D90	90th percentile substrate size	PS<1	Percentage of fine sediment <1 mm
MRPS	Mean riffle particle size	PS16-256	Percentage of area of 16-256 mm substrate
PBS	Percentage of boulder substrate	RS	Substrate rating
PE	Percentage of substrate embeddedness	SSA	Area with suitable spawning substrate
		SSC	Substrate score
PFS	Percentage of fine substrate		
	PHYSICAL (C) - TEMPERATURE		
FFD	Frost-free days	NT5P	Minimum water temperature of 5 previous days
MAT	Mean annual air temperature		
MAWT	Mean annual water temperature	RWT	Water temperature rating
MAXT	Mean annual maximum water temperature	RXST	Maximum summer water temperature rating
		XST	Maximum summer water temperature
	CHEMICAL (C)		
C	Conductivity	NDO	Minimum dissolved oxygen
DOR	Dissolved oxygen range	NN	Nitrate nitrogen
MAL	Mean alkalinity	RCH	Calcium hardness rating
MBOD5	Mean annual 5-day biochemical oxygen demand	RMH	Magnesium hardness rating
		RNN	Nitrate nitrogen rating
MC	Mean conductivity	RPH	pH rating
MPCC	Mean platinum-cobalt color	RPO	Phosphate rating
MTH	Mean total hardness	RSU	Sulfate rating
MTOC	Mean total organic carbon	RT	Turbidity rating
MTP	Mean total phosphorus	RTA	Total alkalinity rating
MTU	Mean turbidity	SU	Sulfate

[a] Letters refer to categories of variables defined in the appendix heading and text.
[b] Flows for specific months were grouped by season.

Table 10—Frequency that independent variables were found significant in 85 models, excluding tests of weighted usable area

Independent variable	Frequency used	Model numbers[a]
Drainage basin variables (A[b]):		
Reach elevation	4	1.04,* 4.07, 4.23, 4.24
Drainage area	4	1.02, 1.03, 4.36, 4.37
Mean basin elevation	3	1.02, 1.03, 1.05*
Channel morphometry variables (B):		
Mean depth	11	2.03, 2.16, 4.02, 4.03, 4.07, 4.27,* 4.29,* 4.30,* 4.32,* 4.33,* 4.39
Mean width	6	1.04,* 2.16, 4.07, 4.23, 4.29,* 4.33*
Surface area	6	2.01, 2.02, 2.03, 4.10,* 4.11,* 4.39
Pool area	4	2.03, 2.04, 4.08, 4.26
Width-to-depth ratio	4	1.05,* 2.16, 4.06, 4.23
Mean pool depth	3	2.03, 2.04, 4.08
Section gradient measured in field	3	2.16, 3.09, 4.07
Flow variables (B):		
Mean monthly flow	5	4.27,* 4.29,* 4.31,* 4.32,* 4.33*
Mean summer flow	3	2.06, 2.07, 2.08
Habitat structure variables (C):		
Area of all cover	8	2.04, 3.04,* 4.01, 4.08, 4.14, 4.36, 4.37, 4.38
Length of undercut bank	4	2.03, 3.03, 3.06, 3.07
Area of overhanging riparian vegetation	3	3.08,* 3.09, 4.39
Area of rubble, boulder, and aquatic vegetation substrate	3	3.06, 3.07, 3.14
Biological variables (C):		
Number of fish species	6	4.27,* 4.30,* 4.32,* 4.33,* 4.34,* 4.35*
Species range	5	4.29,* 4.31,* 4.32,* 4.33,* 4.35*
Physical variables (substrate and temperature, C):		
Percent substrate embeddedness	5	3.18, 3.19, 3.20, 3.21, 3.22
Mean annual water temperature	4	4.27,* 4.30,* 4.32,* 4.33*
Frost-free days	3	4.30,* 4.31,* 4.33*
Mean annual air temperature	3	4.29,* 4.30,* 4.33*
Chemical variables (C):		
Dissolved oxygen range	7	4.27,* 4.28,* 4.29,* 4.30,* 4.31,* 4.33,* 4.35*
pH rating	6	4.15, 4.18, 4.19, 4.20, 4.21, 4.22
Mean alkalinity	4	4.28,* 4.31,* 4.32,* 4.34*
Mean conductivity	4	4.29,* 4.31,* 4.33,* 4.34*
Mean total phosphorus	4	4.28,* 4.29,* 4.31,* 4.33*
Minimum dissolved oxygen	4	4.29,* 4.31,* 4.33,* 4.35*
Mean annual 5-day biochemical oxygen demand	3	4.27,* 4.29,* 4.31*
Mean platinum-cobalt color	3	4.27,* 4.29,* 4.33*
Mean total organic carbon	3	4.28,* 4.29,* 4.33*
Mean turbidity	3	4.31,* 4.32,* 4.33*

[a] Asterisks indicate models with 20 or more degrees of freedom and coefficients of determination larger than 0.50.
[b] Letters refer to categories of variables defined in the appendix heading and text.

☆ U.S. GOVERNMENT PRINTING OFFICE:1988-593-224/80102

Fausch, Kurt. D; Hawkes, Clifford L.; Parsons, Mit G. 1988. Models that predict standing crop of stream fish from habitat variables: 1950-85. Gen. Tech Rep. PNW-GTR-213. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 52 p.

We classified mathematical models that predict standing crop of stream fish from habitat variables by type of independent habitat variable, mathematical structure, and model quality. The 99 models reviewed were grouped by the types of independent variables found significant during model development: (A) drainage basin variables (5 models), (B) channelmorphometry and flow variables (16 models), (C) habitat-structure, biological, physical, and chemical variables (25 models), (D) a combination of several variable types (39 models), and (E) tests of weighted usable area as a habitat model (14 models). We found that sound statistical procedures were often neglected during development of models. Frequent problems were small sample size, possible bias caused by error in measuring habitat variables, using poor methods for choosing the best model, not testing models, using observational models to predict standing crop, and using unrealistic assumptions in estimating standing crop. The major biological assumption that the fish population was limited by habitat rather than by fishing mortality, interspecific competition, or predation also usually was not addressed. To be useful for analyzing land management alternatives, models must include variables affected by management and be specific for a homogeneous area of land.

Keywords: Stream fish, fish habitat, predictive models, stream-fish standing crop.

Pacific Northwest Research Station
319 S.W. Pine St.
P.O. Box 3890
Portland, Oregon 97208

U.S. Department of Agriculture
Pacific Northwest Research Station
319 S.W. Pine Street
P.O. Box 3890
Portland, Oregon 97208

Official Business
Penalty for Private Use, $300

BULK RATE
POSTAGE +
FEES PAID
USDA-FS
PERMIT No. G-40

Do NOT detach Label